

A COMPARATIVE MORPHOLOGICAL STUDY OF THE HINDWING VENATION OF THE ORDER COLEOPTERA, PART II^{1 2}

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Abstract.—Specialization trends were determined from a study of the comparative morphology of the hindwing venation of 82 families of the order Coleoptera. Many of the family relationships involved a comparison of anal patterns. The overall trend consisted of a reduction in venation accompanied by a fusion of longitudinal veins, which in turn resulted in a crossvein appearing pattern.

Various lines of specialization were established based on a comparison of preanal venation, the number of anal veins, the presence or absence of a wedge cell and such general features as wing outline, radial cell configuration, etc. Through the results of such an approach lead to developing the following lines of specialization: Archostemata–Adephaga, Hydrophilidae–Scarabaeoidea, Staphylinidae, Dermestidae, Buprestidae, Elateridae–Cantharidae, Dryopidae–Byrrhidae, Chrysomelidae–Bostrichidae, Lymexyloidae–Meloidea–Tenebrionidae, and the Cucujoidea–Curculionidae.

The following discussion is based on an analysis of information received as a result of comparative studies involving the coleopterous families, parallel trends observed in the Cerambycidae and Buprestidae, and a direct comparison to the coleopterous–megalopterous comparative pattern proposed by Wallace and Fox (1975). Comparative wing patterns are included to serve mainly as guides in the discussion of the various specializations.

It is believed that although much can be derived from the evidence at

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hand, too specific an interpretation based on reduced venation leads largely to speculation. Certain specific family relationships can only be interpreted with some degree of confidence in the light of more detailed serial studies.

Studies conducted by Good (1925) on the Buprestidae and Good (1929) on the Cerambycidae, serve as examples of such detailed serial studies and are therefore significant parallel guides to specialization trends in the Coleoptera as a whole. Other approaches involve the morphological investigations by Hamilton (1971, 1972) and the use of multiple metathoracic wing structures in the study of the phylogeny of Adephaga by Ward (1979).

Corrections on the anal vein homology of the Bostrichidae drawings illustrated in Part I by Wallace and Fox (1975) are included. The change involves the loss of the vein postcubitus. The details are discussed under the Cupedidae-Adephaga (Figs. 14-26) and Chrysomelidae-Bostrichidae (Figs. 138-139, 141) sections.

FAMILY SPECIALIZATION TRENDS

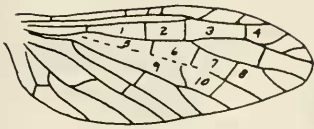
Cupedidae-Adephaga (Figs. 12-26).—For purposes of comparison, arbitrary numbers have been assigned to the cellular nature of both the preanal pattern of Cupedidae-Adephaga (Fig. 3) and the comparative coleopterous-megalopterous pattern (Fig. 2). Sialidae (Fig. 1) is included to emphasize the line of development along which Coleoptera has paralleled.

The fusion apically of R_s with R_1 has resulted in the formation of the large cellular space in the Cupedidae. Associated with the fusion of R_s with radius, there is a loss of two radial crossveins with the retention of the third one beyond the C-D fold. This has resulted in the formation of the cell designated 1+2+3. Cell number 4 is a result of the fusion of R_2 with R_1 and the subsequent fusion of these veins with subcosta. This is based primarily upon a study of Adephaga (Figs. 10-11). With the fusion of R_2 and R_1 , R_3 is therefore the vein which runs freely to the apical margin of the wing. Cells 5, 6 and 7 in the Cupedidae are formed from three radio-medial crossveins. The distal side of cell 8 is formed in series with the stem of $R_{4+5}+MA$ and a fourth radio-medial crossveins (Figs. 6-9). The retention of $R_{4+5}+MA$ is based upon the possession of a remnant of this stem as it appears in the Carabidae (Fig. 25) and Cicindelidae (Figs. 11, 26).

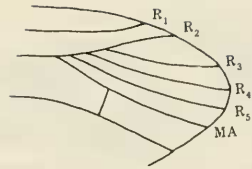
Cell 9 is the same as occurs in the comparative coleopterous-megalop-

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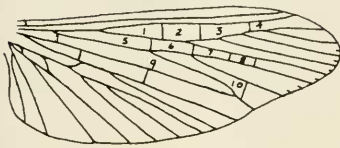
Figs. 1-10. 1, Sialidae cellular pattern. 2, Comparative coleopterous cellular pattern. 3, Cupedidae-Adephaga comparative cellular pattern. 4, Polyphaga comparative cellular pattern. 5, Directional wing pattern. 6, Cupedidae-Adephaga comparative apical pattern, Series 1. 7, Cupedidae-Adephaga comparative apical pattern, Series 2. 8, Cupedidae-Adephaga comparative apical pattern, Series 3. 9, Cupedidae-Adephaga comparative apical pattern, Series 4. 10, *Gyrinus fraternus* Couper (Gyrinidae).



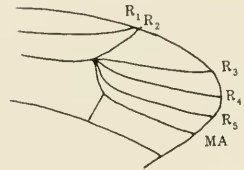
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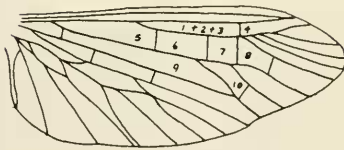
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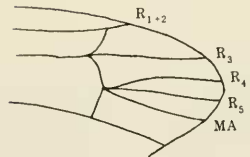
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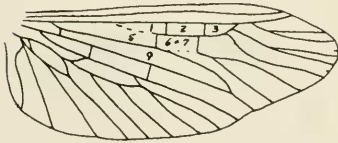
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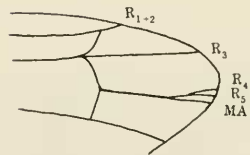
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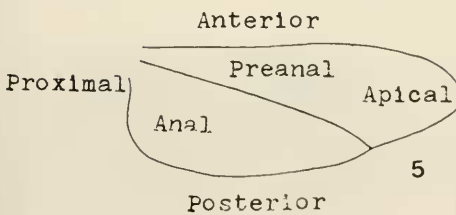
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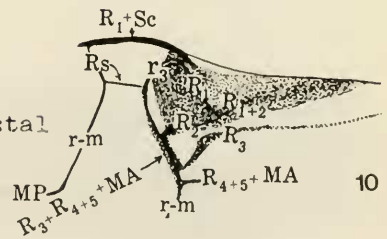
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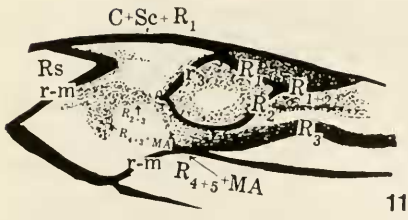
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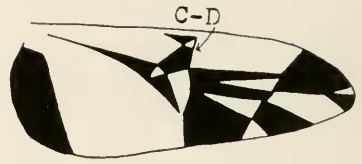
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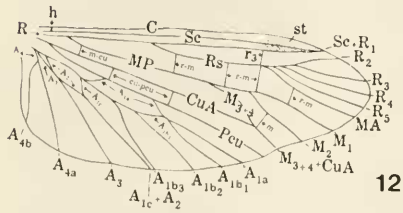
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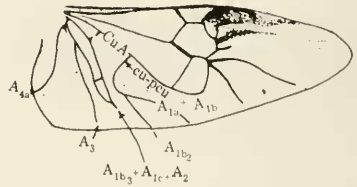
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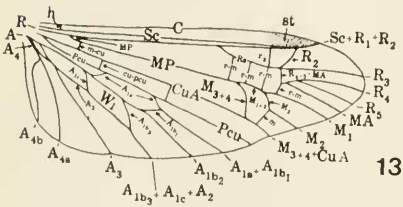
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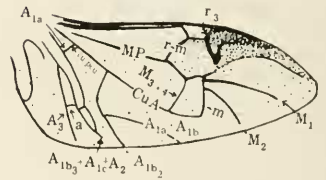
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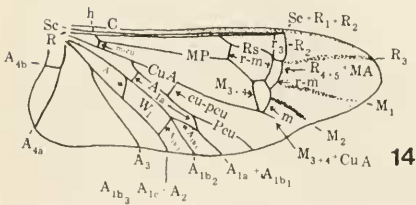
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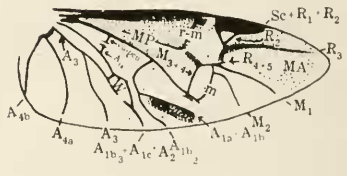
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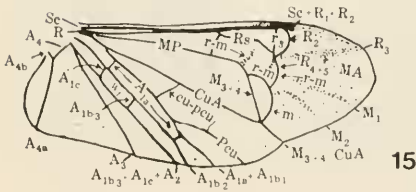
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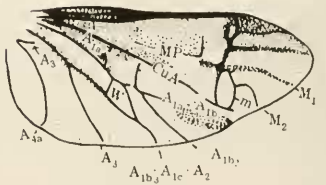
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terous pattern and has as its boundaries a proximal m-cu crossvein, MP, CuA, and the fusion of M_{3+4} with CuA. This cell appears larger in the Cupedidae due to the fusion distally of M_{3+4} with M_{1+2} .

The number 10 cell of the Cupedidae and the Adephaga consists of the fusion distally of branches M_{1+2} , the serial connection of M_2 and a medial crossvein with the subsequent fusion of this series to $M_{3+4}+CuA$.

In the Cupedidae (Fig. 14), the anal pattern involves a coalescence of the anal veins as compared to the comparative coleopterous-megalopterous pattern of Wallace and Fox (1975). This consists of a fusion of A_{1a} with A_{1b_1} and a fusion of A_{1b_3} with $A_{1c}+A_2$ forming what has been designated the wedge cell (W). In comparison to the Scarabaeidae (Fig. 45), only the transverse portion of A_{4b} is retained.

Much of the discussion of the Adephaga follows that of King (1956). He discusses the homogeneity of the wing pattern as exhibited by this suborder. Although the overall pattern of the Adephaga is more specialized than that of the Cupedidae, certain families of this suborder contain generalized features. Such features as previously mentioned involve the possession of a $R_{4+5}+MA$ stem in the Carabidae and a well developed A_{4b} in the Dytiscidae (Fig. 19).

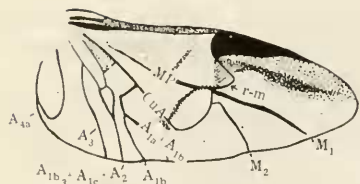
In general, specialization trends in the preanal area of the Adephaga involve a partial loss of the Rs in the area of the C-D fold, a reduction in the number of radio-medial crossveins and a tendency toward the gradual atrophy of the proximal segment of MP as well as $M_{3+4}+CuA$ distal to the medial crossvein. Furthermore, Carabidae and Cicindelidae progressively exhibit a loss of cell 10 due to the gradual fusion of M_2 to $M_{3+4}+CuA$ accompanied by a loss of the medial crossvein.

In comparison to the anal pattern traced in the Polyphaga (Figs. 92, 101, 149), the families of Adephaga share the line of specialization involving the formation of the wedge cell accompanied by the loss of Pcu. The homology of the anal veins therefore are from anterior to posterior: $A_{1a}+A_{1b_1}$, A_{1b_2} , $A_{1b_3}+A_{1c}+A_2$, A_3 , A_{4b} .

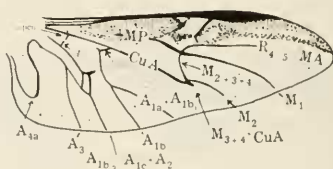
The generalized pattern of the Adephaga as a whole is seen in the Gyrinidae (Fig. 17), Dytiscidae (Fig. 19), Amphizoidae (Fig. 20), Hygrobiidae (Fig. 21), and Noteridae (Fig. 22).

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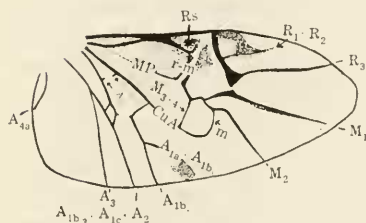
Figs. 11–20. 11, *Cicindela sexguttata* F. (Cicindelidae). 12, Comparative Cupedidae–Adephaga pattern, Series 1. 13, Comparative Cupedidae–Adephaga pattern, Series 2. 14, *Priacma serrata* (LeConte) (Cupedidae). 15, *Cupes concolor* Westwood (Cupedidae). 16, *Harpalus caliginosus* (F.) (Carabidae), folding pattern. 17, *Dineutus assimilis* (Kirby) (Gyrinidae). 18, *Dineutus vittatus* (Germar) (Gyrinidae). 19, *Agabus lugens* (LeConte) (Dytiscidae). 20, *Amphizoa insolens* LeConte (Amphizoidae).



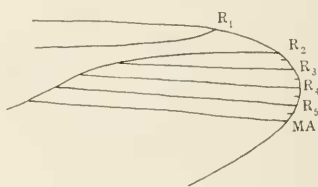
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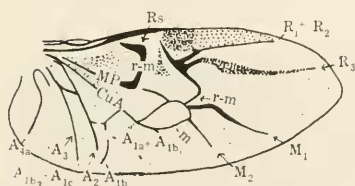
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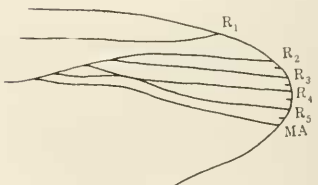
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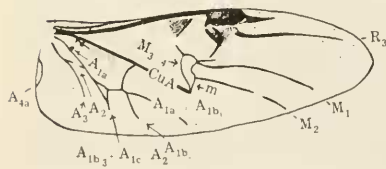
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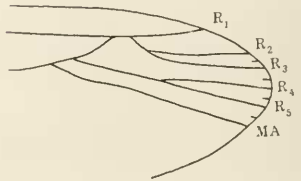
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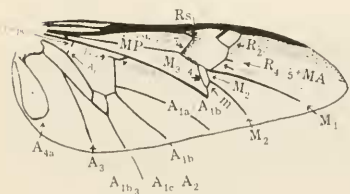
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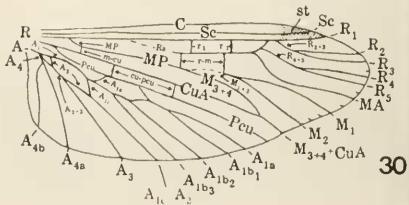
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Certain lines of specialization within the Adephaga involve the following:

1. There is in the Rhysodidae (Fig. 24) a tendency toward the reduction in size of the W cell. This is due to the gradual fusion of A_{1b_3} with $A_{1c}+A_2$. In the Haliplidae (Fig. 23) complete fusion occurs with the subsequent loss of any wedge cell. Therefore both Rhysodidae and Haliplidae share this specialization with the eventual loss of the free portion of A_{1c} .

2. The Carabidae and Cicindelidae (Figs. 25–26) share an overall common pattern. Specifically it may be noted that both possess a well developed postcubital spur and show a tendency toward a reduction in the size of the number 10 cell. This reduction in size is the result of a narrowing of the space between M_{3+4} and M_2 . Thus as noted in Cicindelidae (Fig. 26), there is the eventual loss of the medial crossvein and the complete fusion of M_{3+4} and M_2 with the subsequent loss of cell 10.

3. In the Gyrinidae (Figs. 17–18) there occurs in *Dineutes vittatus* (Germar) an apparent crossvein between $A_{1c}+A_2$ and A_3 . In comparison to the venational variation in species of Cebriionidae (Fig. 85), this condition is an accessory branching of $A_{1c}+A_2$ with the subsequent fusion of this vein with A_3 .

The following discussion of the polyphagan patterns (Figs. 4, 27–30) is a comparison of the preanal and anal venation in which are included characteristics shared with the Cupedidae and Adephaga as well as specializations involving the suborder as a whole. As noted in the Scarabaeidae (Fig. 43), the subcosta and radius do not fuse apically. There also remains much of the cellular portion of the Cupedidae as is noted in the Cebriionidae (Fig. 78). Cells 2 and 3 are present due to the retention of the first and second radial crossveins. Cell 4 is lost as a result of R_{2+3} of the radial sector fusing with R_1 . This in turn leads to a loss of the third radial crossvein present in the adephagan pattern. Cells 6 and 7 are present as a fused cell in the Cebriionidae due to the loss of a second radio-medial crossvein. Cell 8 is interpreted as open distally due to the atrophy of the distal radio-medial crossvein. Cell 10 also is open distally due to the loss of the medial crossvein, which was present in the Cupedidae and Adephaga.

It becomes apparent by comparison to the Elateroidea (Figs. 78, 85–86) there are two radial crossveins occurring before the C–D fold. As mentioned

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Figs. 21–30. 21, *Hygrobia hermanni* (F.) (Hygrobiidae). 22, *Hydrocanthus iricolor* Say (Noteridae). 23, *Peltodytes muticus* (LeConte) (Haliplidae). 24, *Rhysodes* sp. (Rhysodidae). 25, *Calosoma sycophanta* L. (Carabidae). 26, *Cicindela sexguttata* F. (Cicindelidae). 27, Polyphaga comparative apical pattern, Series 1. 28, Polyphaga comparative apical pattern, Series 2. 29, Polyphaga comparative apical pattern, Series 3. 30, Polyphaga comparative pattern, Series 1.

previously these form cells 2 and 3. The closing of cell 3 was considered by Forbes as the result of a fusion of a radial crossvein with the radial sector. This particular condition assumes a fusion of the two but is not clearly present in any of the wings studied. Therefore, in comparison to the consistent pattern of the three radial crossveins in Megaloptera, the Polyphaga possess two radial crossveins before the C-D fold and the Adephaga a third one beyond the C-D fold. It appears in the Polyphaga that the first radial crossvein is variable in its position and the second radial crossvein atrophies resulting in the formation of the 2+3 cell (i.e. radial cell by previous authors).

A characteristic pattern in the Polyphaga is the gradual atrophy of the base of Rs and MP. Previous authors have designated these backward projecting spurs as radial recurrent (Rr) and medial recurrent (Mr) respectively.

As discussed in relationship to the comparative coleopterous-megalopterous pattern, the apical venation is difficult to trace as a result of the loss of much of the venation in many polyphagan families, as well as the unusual patterns developed due to folding. Even though folding alters the venation in the apical area, it retains as its basis the pectinate megalopterous pattern.

In the Polyphaga, specialization of the media as opposed to the Adephaga involves the atrophy of the proximal segment of M_{1+2} , producing the characteristic spurious vein indicative of the Chrysomeloidea. A similar specialization is seen between cells 7 and 10 in the Sialidae (Fig. 1).

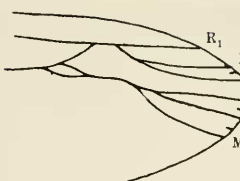
The anal venation is the same as that of the comparative coleopterous-

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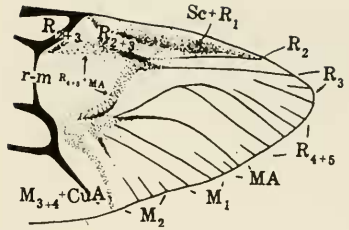
Figs. 31-40. 31, Hydrophilidae comparative apical pattern, Series 1. 32, Hydrophilidae comparative apical pattern, Series 2. 33, Hydrophilidae comparative pattern, Series 1. 34, Hydrophilidae comparative pattern, Series 2. 35, *Hydrous triangularis* (Say) (Hydrophilidae). 36, *Hydrous triangularis* (Say) (Hydrophilidae). 37, Scarabaeoidea comparative pattern. 38, *Dendroblyx earlii* (Levin) (Lucanidae). After Holloway, 1963. 39, *Certognathus gibbosus* (Broun) (Lucanidae). After Holloway, 1963. 40, *Pinotus carolinus* (L.) (Scarabaeidae).

Figs. 41-50. 41, *Xyloryctes jamaicensis* (Drury) (Scarabaeidae). 42, *Xyloryctes jamaicensis* (Drury) (Scarabaeidae). 43, *Aphodius denticulatus* Haldeman (Scarabaeidae). 44, *Canthon probus* (Germar) (Scarabaeidae). Distal branching of M and CuA. 45, *Euphoria herbacea* (Olivier) (Scarabaeidae). 46, *Dichelonyx vicina* Fall (Scarabaeidae). 47, *Trichiotinus bibens* (F.). 48, *Pleocoma behrensi* LeConte (Scarabaeidae). 49, *Cloeotus aphodioides* (Illiger) (Scarabaeidae). 50, *Popilius disjunctus* (Illiger).

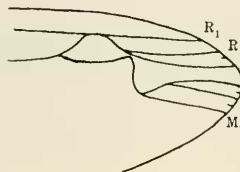
Figs. 51-60. 51, Histeridae comparative pattern. 52, *Hister inaequalis* Olivier (Histeridae). After Forbes, 1922. 53, *Hister abbreviatus* F. (Histeridae). 54, *Pinotus carolinus* (L.) (Scarabaeidae). 55, Staphylinoida comparative pattern. 56, *Silpha discicollis* Brulle (Silphidae). 57, *Nicrophorus orbicollis* Say (Silphidae). 58, *Staphylinus maculosus* Gravenhorst (Staphylinidae). 59, Polyphaga comparative pattern, Series 2. 60, Dermestidae comparative pattern, Series 1.



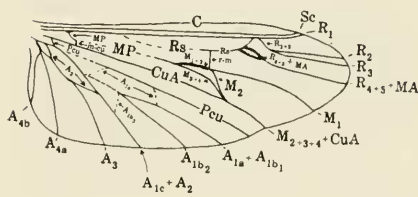
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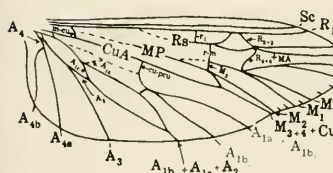
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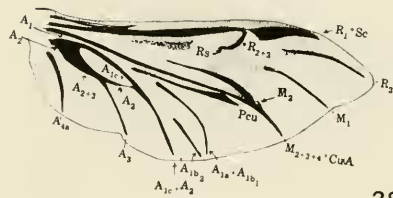
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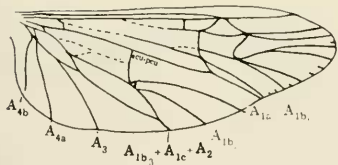
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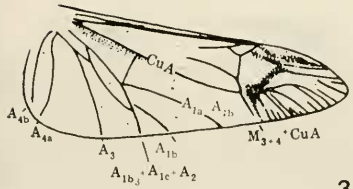
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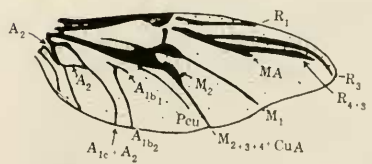
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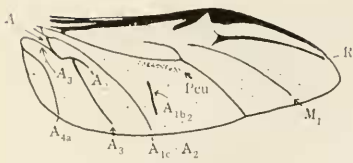
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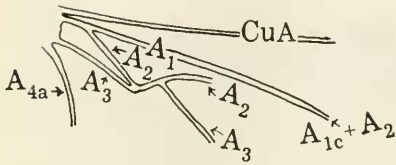
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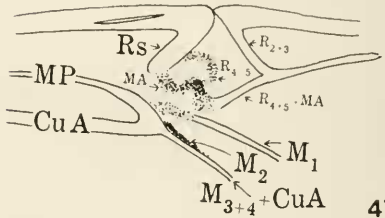
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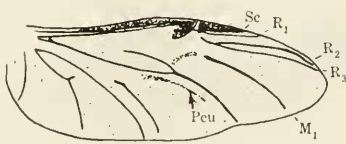
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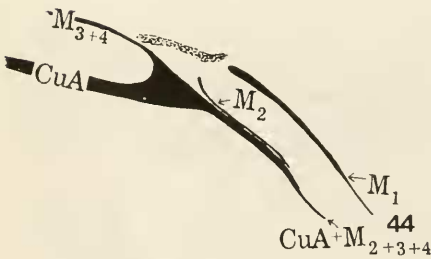
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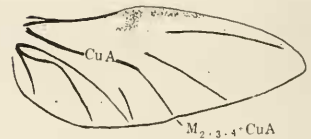
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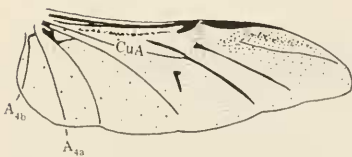
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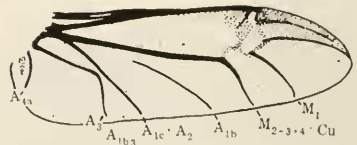
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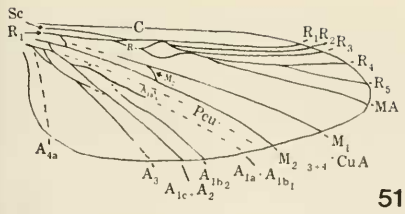
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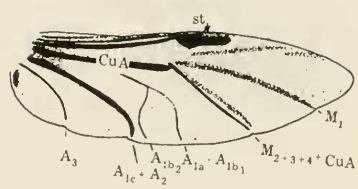
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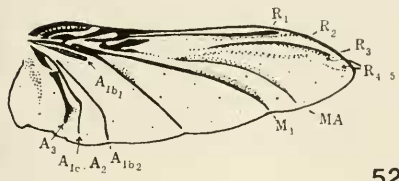
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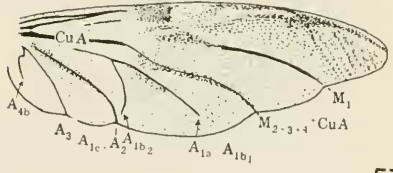
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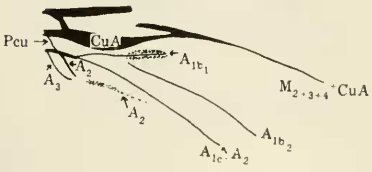
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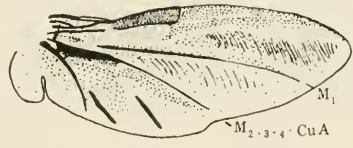
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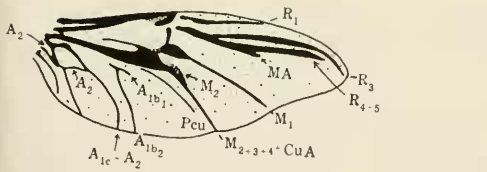
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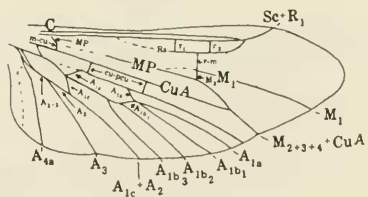
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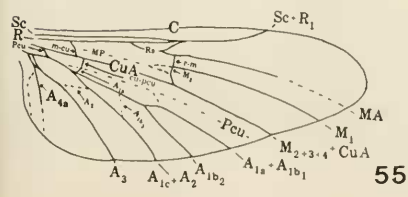
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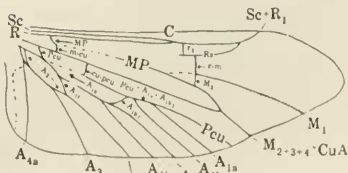
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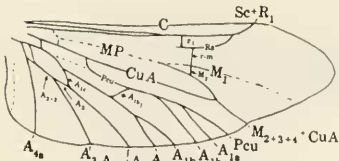
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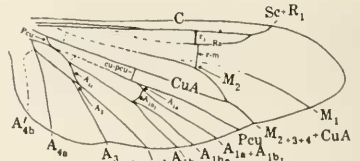
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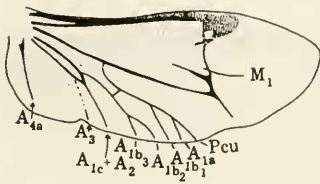
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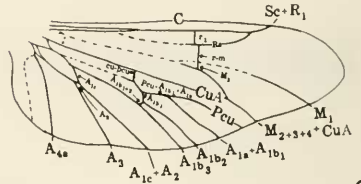
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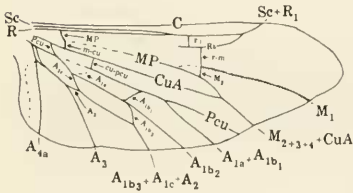
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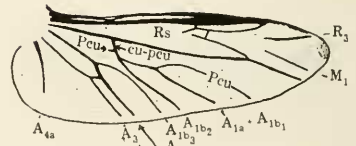
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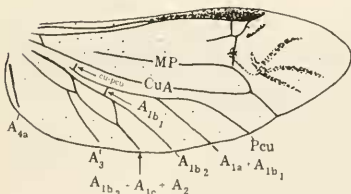
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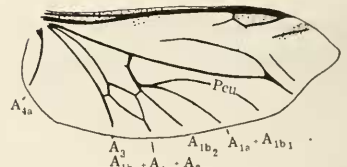
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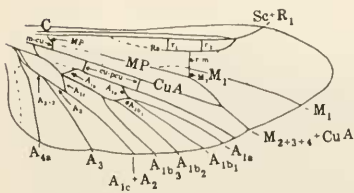
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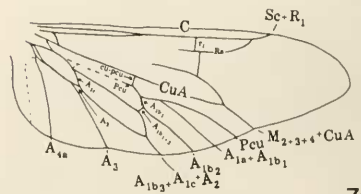
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megalopterous pattern and serves as a basis for comparison of the anal patterns of both the Adephaga and Polyphaga.

The following involves a comparison of the lines of specialization as represented by the families of the suborder Polyphaga and their relationship to the comparative polyphagan pattern (Fig. 30).

Hydrophilidae (Figs. 31–35).—The apical venation (Fig. 36), as discussed earlier, consists of a large number of accessory veins, but retains a modification of the basic pectinate pattern paralleled in the Megaloptera. The manner in which R_{4+5} and MA touches R_3 and forms a portion of the complex apical pattern with M_1 is derived largely from a comparative study of both the Hydrophilidae pattern and the Scarabaeidae (Figs. 46–49). M_2 is independent from $M_{3+4}+CuA$.

The anal area may be compared to a condition that is paralleled in the Cerambycidae (Fig. 111). Comparing this type of pattern to that of the Polyphaga comparative pattern (Fig. 30) specializations involve the following:

1. The fusion of A_{1a} and A_{1b_1} , as is interpreted in the Cupedidae (Fig. 14) and Cerambycidae (Fig. 110).

2. A loss of A_{1b_3} .

3. A fusion of A_{1b_3} with A_{1c} and A_2 forming the wedge cell.

4. The further fusion of the A_{1b_2} with that of $A_{1b_3}+A_{1c}+A_2$.

5. The fusion of A_{1b_2} has pulled a segment of $A_{1a}+A_{1b_1}$ toward the W cell. As paralleled in much of the Adephaga (Figs. 21–22), the large apparent cu–pcu crossvein is a serial segment of cu–pcu in alignment with proximal segment of $Pcu+A_{1a}$.

6. Although there appears to be a slight fusion of the proximal segment of A_4 with A_{2+3} , there remains in the generalized condition the branches A_{4a} and A_{4b} .

Scarabaeoidea (Figs. 37–50).—Although this group shares in common with the Hydrophilidae the possession of an apical pattern, the accessory venation is not apparent.

The cell 2+3 opens proximally as a result of the preanal specialization consisting of a loss of the r_1 crossvein.

Aside from the usual loss of the proximal segment of Rs and MP, there

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Figs. 61–70. 61, Dermestidae comparative pattern, Series 2. 62, *Megatoma giffardi* (Blaisdell) (Dermestidae). After Beal, 1967. 63, Dermestidae comparative pattern, Series 3. 64, *Dermestes lardarius* L. (Dermestidae). 65, Polyphaga comparative pattern, Series 2. 66, Buprestidae comparative pattern, Series 1. 67, Buprestidae comparative pattern, Series 2. 68, *Dicerca lurida* (F.) (Buprestidae). After Forbes, 1922. 69, *Dystaxia murrayi* LeConte (Buprestidae). After Good, 1925. 70, Dascillidae–Rhhipiceridae comparative pattern.

is no evidence of the branch MA. There is a retention of a strong M_1 with a tendency toward the fusion of M_2 with $M_{3+4}+CuA$.

The anal pattern in both the Lucanidae (Fig. 38) and the more generalized Scarabaeidae (Fig. 40) is characterized largely by a trend involving a reduction in venation.

In many cases Pcu in Scarabaeidae is a weakly developed vein occurring only as a sclerotized trace near CuA (Figs. 41–43). There has been a complete loss of any free portion of A_{1a} . A_{1a} exists as a fused part of A_{1b_1} . The free forked vein A_{1b_1} and A_{1b_2} has lost its attachment to A_{1c} . As paralleled in the Elateroidea, there is the loss of A_{1b_3} . The remaining venation (Figs. 41–42), which includes A_2 and A_3 and the forking of A_4 , served as a basis for the determination of the proximal pattern of these veins in the comparative coleopterous–megalopterous venation.

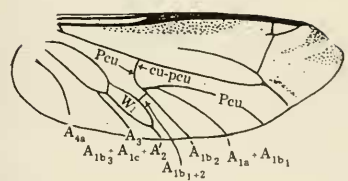
Passalidae (Fig. 50), as a result of other characteristics, has a close affinity to the Scarabaeidae, however the venation is highly reduced. This is evident in the loss of any recognizable free segment of MP (Mr) and the highly reduced Rs (Rr) and anal pattern. However, as a result of a study of a series of Scarabaeidae, it was noted that a parallel example of such a specialization occurs in the scarab *Cloeotus aphodioides* (Illiger) (Fig. 49). In the absence

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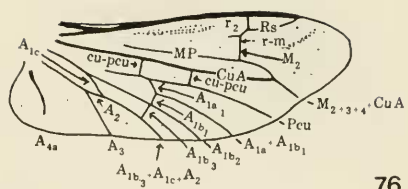
Figs. 71–80. 71, *Dascillus davidsoni* LeConte (Dascillidae). 72, *Sandalus niger* Knoch (Rhypiceridae). 73, Polyphaga comparative pattern, Series 2. 74, Elateroidea–Cantharoidea–Dryopoidea comparative pattern. 75, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Generalized pattern. 76, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. After Forbes, 1922. 77, *Telephorus* sp. (Lampyridae). Folding pattern. After Forbes, 1924. 78, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 79, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 80, *Scaptolenus lecontei* (Sallé) (Cebrionidae).

Figs. 81–90. 81, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 82, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 83, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 84, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 85, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 86, *Scaptolenus lecontei* (Sallé) (Cebrionidae). Pattern of individual variation in the species. 87, *Photinus pennsylvanica* (DeGeer) (Lampyridae). 88, *Lucidota currusca* (L.) (Lampyridae). 89, *Photinus pyralis* (L.) (Lampyridae). Pattern of individual variation in the species. 90, *Photinus pyralis* (L.) (Lampyridae). Generalized pattern.

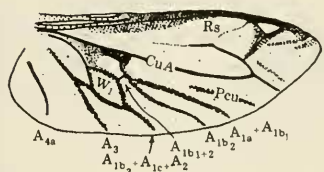
Figs. 91–100. 91, *Ludius hamatus* (Say) (Elateridae). 92, *Adelocera profusa* Candize (Elateridae). 93, *Phengodes laticollis* LeConte (Phengodidae). 94, *Calopteron reticulatum* (F.) (Lycidae). 95, *Chauliognathus marginatus* F. (Cantharidae). 96, *Perothops mucida* (Gyllenhal) (Perothopidae). 97, *Isorhipis ruficornis* (Say) (Eucnemidae). 98, *Lara avara* LeConte (Elmidae). After Hinton, 1940. 99, Dryopidae composite pattern. 100, *Dryops viennensis* Castelman (Dryopidae). After Forbes, 1922.



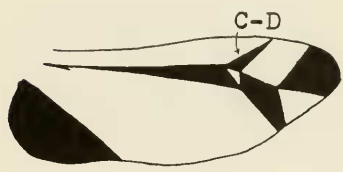
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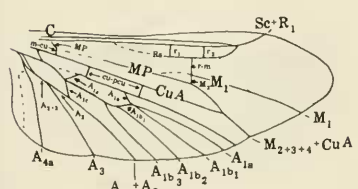
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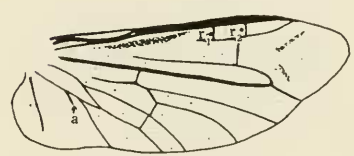
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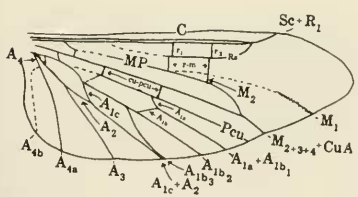
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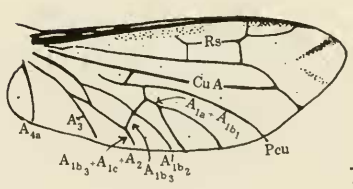
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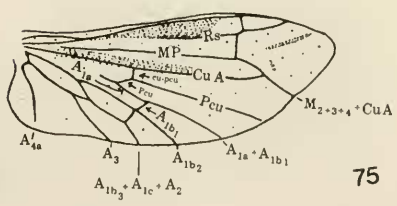
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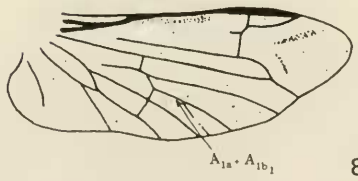
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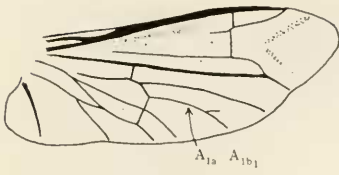
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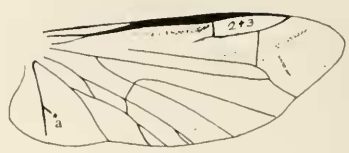
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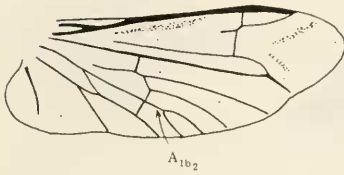
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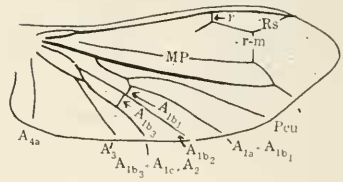
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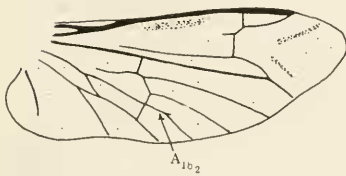
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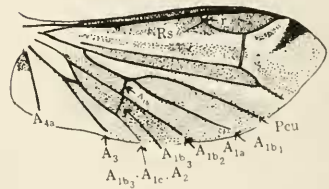
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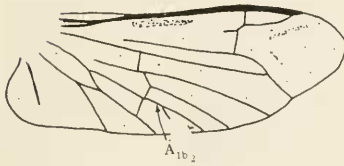
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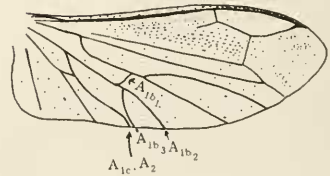
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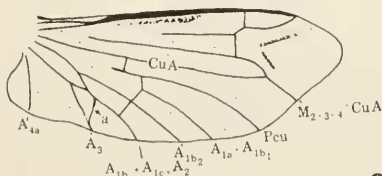
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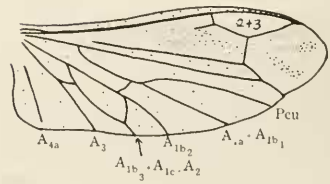
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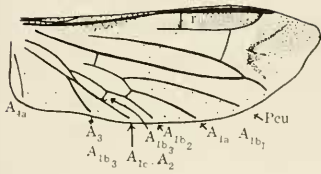
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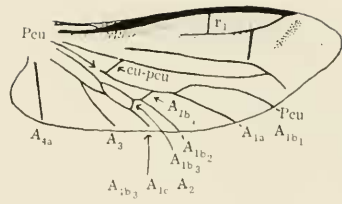
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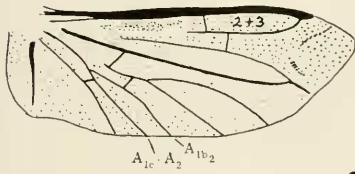
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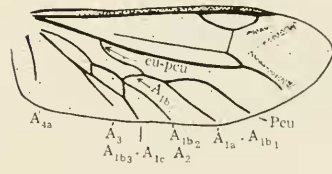
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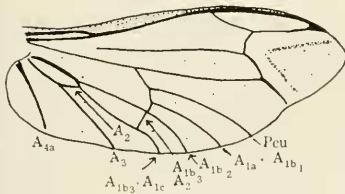
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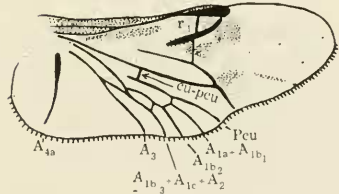
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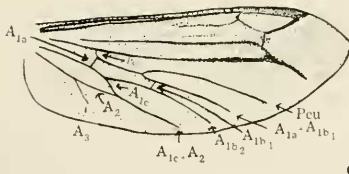
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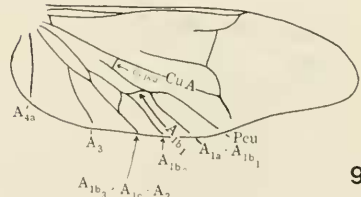
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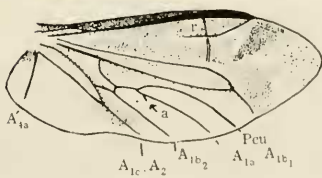
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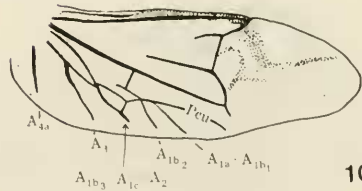
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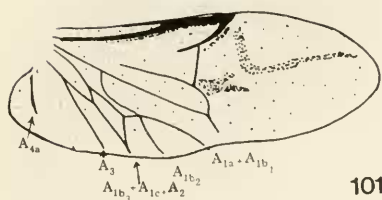
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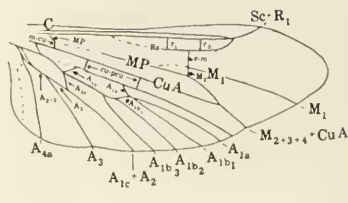
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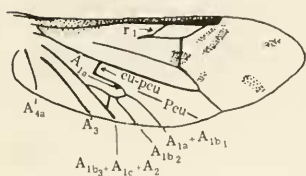
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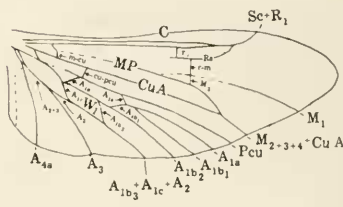
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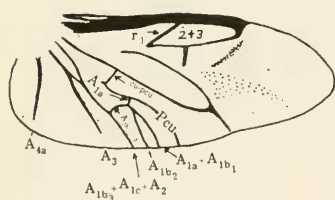
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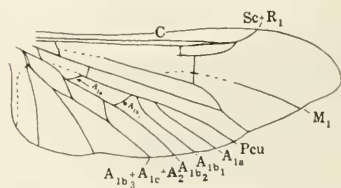
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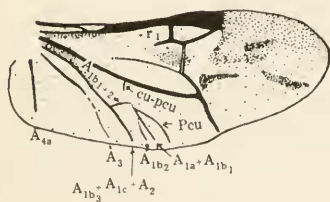
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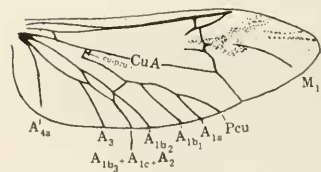
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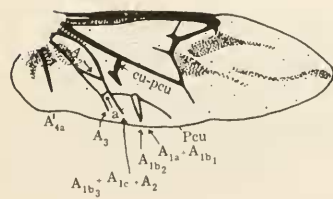
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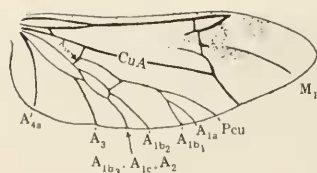
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of serial studies, such an approach in selecting a parallel study of this nature indicates the venational relationship of a family, which on the basis of reduced venation does not appear to have any direct venational relationship to the group in which it has been placed on the basis of other characters.

Histeroidea (Figs. 51–53).—As indicated by Forbes (1922), the Histeridae have retained both a radial and medial recurrent. Particularly noteworthy is what Graham (1922) referred to as a pushing of the primary venation basad. The anal pattern (Fig. 53) parallels much of what is seen in the Scarabaeidae (Fig. 54). As is indicative of the more highly specialized Scarabaeidae, there is a loss of any trace of a Pcu. Although the Histeridae possess a somewhat unusual pattern, it is believed that due to the retention of a relatively well developed apical venation, as well as a sharing of a similar anal pattern, much of the histerid venation is not unlike that which is found in the Scarabaeidae as well as that of the Staphyloidea.

Staphyloidea (Figs. 56–58).—In the discussion of this particular group, Forbes (1922) pointed out that due to the highly reduced nature of the venational pattern, there is nothing to connect this series with any existing group. The absence of both a well developed radial cell and a medial recurrent would suggest a highly specialized pattern paralleling that found in the scarab *C. aphodioides* (Illiger) (Fig. 49) and in that of the Passalidae (Fig. 50). The families included in this group are placed together on the basis of sharing an overall common pattern. Although an attempt is made to suggest a common pattern (Fig. 55) in which there is some degree of affinity of this group to other families of Coleoptera, much of what is presented is the result of parallel specialization trends occurring in other families, notably the Scarabaeidae.

The Staphyloidea possess in common with the Scarabaeidae and Histeridae traces of an apical venation with the retention of a well developed M_1 in such forms as *Silpha* (Fig. 56).

The anal pattern, though reduced, consists of an alignment of the proximal segment of A_{1a} and cu-pcu crossvein ("anal arculus" of Forbes, 1922). In addition, there is the complete loss of Pcu as paralleled in the more highly specialized Scarabaeidae. Therefore, the anal vein which undergoes forking in both *Silpha* (Fig. 56) and *Nicrophorus* (Fig. 57) consists of a part of the

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Figs. 101–110. 101, *Helichus lithophilus* (Germar) (Dryopidae). 102, *Ptilodactyla serricollis* (Say) (Ptilodactylidae). 103, *Chelonarium lecontei* Thomson (Chelonariidae). 104, *Psephenus herricki* DeKay (Psephenidae). 105, *Byrrhus cyclophorus* Kirby (Byrrhidae). 106, Polyphaga comparative pattern, Series 2. 107, Cerambycidae comparative pattern, Series 1. 108, Cerambycidae comparative pattern, Series 2. 109, *Parapachyta quadrimaculata* (L.) (Cerambycidae). After Good, 1929. 110, *Pachyta liturata* Kirby (Cerambycidae). After Good, 1929.

branching of A_1 . In comparison to both the Scarabaeidae and the overall specialization trends in the Coleoptera, the anterior branch of this vein consists of a fused portion of A_{1a} and A_{1b_1} . The remaining part consists of the free proximal segment of A_{1b} and the posterior branch A_{1b_2} . In addition to the loss of A_{1b_3} , as paralleled in the Elateroidea (Fig. 92), there is a loss of the free portion of A_2 thus forming the vein $A_{1c} + A_2$ which in *Silpha* consists of a thickened singular appearing vein.

In *Silpha* the remaining anal vein is A_3 . In the genus *Nicrophorus* there is a remnant of A_{1a} .

Dermestoidea (Figs. 59–64).—This group as represented by the Dermestidae possess the largest number of free anal veins of any family of Coleoptera. Although coalescence in *Megatoma* (Fig. 62) has not taken place apically, specializations have involved the fusion of $A_{1a} + A_{1b_1}$ with Pcu as paralleled in the Cerambycidae (Fig. 109). This condition is accompanied by the loss of the free distal portion of A_{1a} . As paralleled in the Bostrichidae, Sphindidae, and Cerambycidae, the Dermestidae retain a remnant of the apical branch of M_1 .

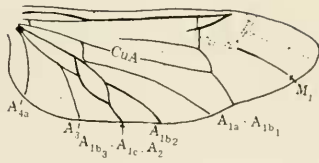
The Dermestidae pattern as indicated by *Dermestes lardarius* L. (Fig. 64) represents a separate line of specialization in which there is the complete fusion of A_{1a} and A_{1b_1} . In addition there is the coalescence of A_{1b_3} with $A_{1c} + A_2$ forming the W cell.

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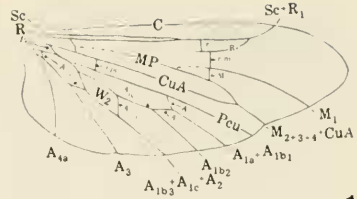
Figs. 111–120. 111, *Eragates spiculates* LeConte (Cerambycidae). After Good, 1929. 112, *Rhagium lineatum* Olivier (Cerambycidae). After Good, 1929. 113, *Atimia dorsalis* LeConte (Cerambycidae). After Good, 1929. 114, *Parapachyta spurca* (LeConte) (Cerambycidae). After Good, 1929. 115, *Migodus tetropiodes* Fairmaire (Cerambycidae). After Crowson, 1955. 116, Sphindidae, Colydiidae, Cucujidae and Curculionidae comparative pattern, Series 1. 117, Sphindidae, Colydiidae, Cucujidae and Curculionidae comparative pattern, Series 2. 118, *Sphindus grandis* Hampe (Sphindidae). After Crowson, 1955. 119, *Coxelus guttulatus* LeConte (Colydiidae). 120, *Cucujus clavipes* F. (Cucujidae).

Figs. 121–130. 121, *Antherophagus ochraceus* Melsheimer (Cryptophagidae). 122, *Belus* sp. (Curculionidae). After Crowson, 1955. 123, *Rhynchites bicolor* F. (Curculionidae). 124, *Helota vigorsi* M'Leay (Helotidae). 125, Byturidae, Biphyllidae, Chrysomelidae, Bostrichidae and Tenebrionoidea comparative pattern. 126, Byturidae–Biphyllidae comparative pattern, Series 1. 127, Byturidae–Biphyllidae comparative pattern, Series 2. 128, Byturidae–Biphyllidae comparative pattern, Series 3. 129, *Byturus unicolor* Say (Byturidae). 130, *Diplocoelus foveolatus* (Reitter) (Biphyllidae).

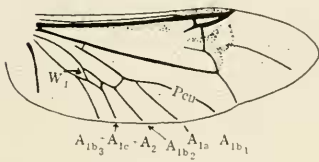
Figs. 131–140. 131, *Eucicones marginalis* (Melsheimer) (Colydiidae). 132, *Diplocoelus brunneus* LeConte (Colydiidae). 133, *Oxyaemus californicus* Crotch (Colydiidae). 134, Coccinellidae comparative pattern. 135, *Cycloneda sanguinea* (L.) (Coccinellidae). 136, *Aphorista vittata* (F.) (Endomychidae). 137, Chrysomelidae comparative pattern. 138, *Euryope* sp. (Chrysomelidae). After Crowson, 1964. 139, *Lema trilineata* (Olivier) (Chrysomelidae). 140, Bostrichidae comparative pattern.



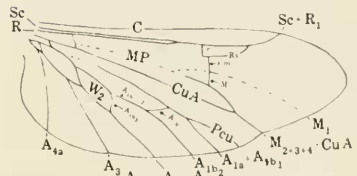
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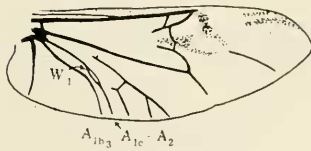
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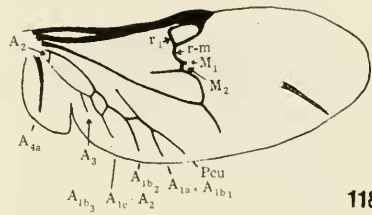
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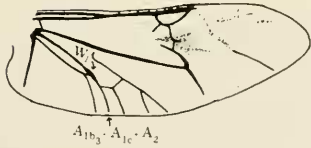
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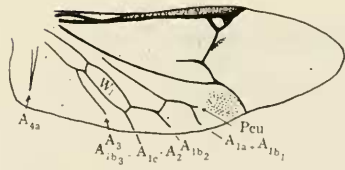
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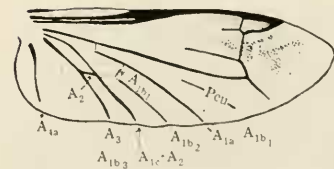
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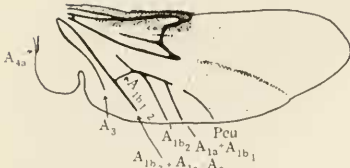
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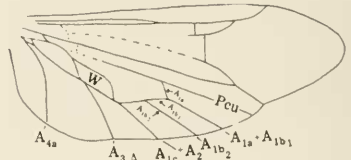
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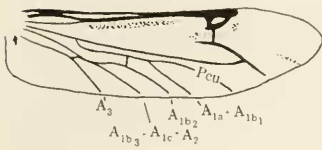
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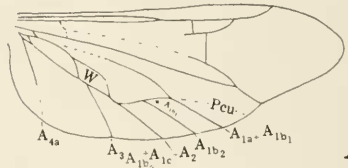
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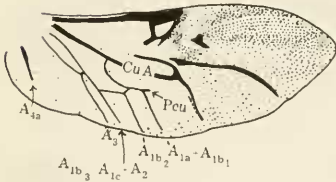
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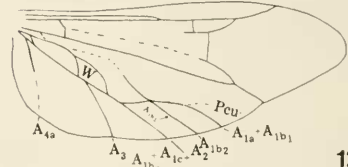
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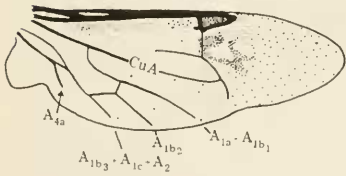
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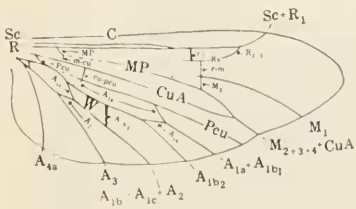
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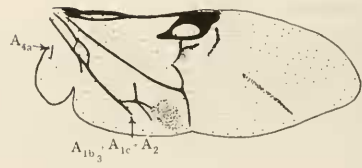
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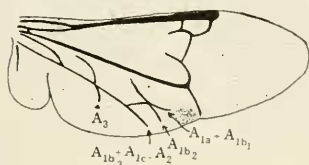
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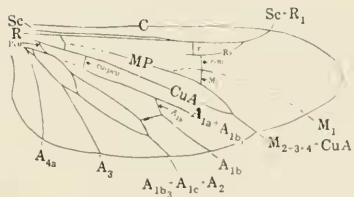
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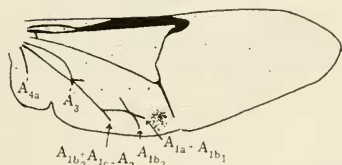
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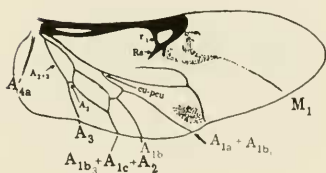
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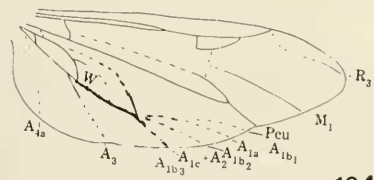
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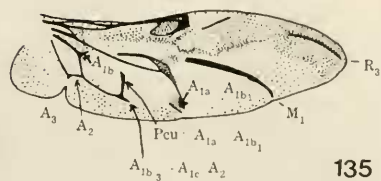
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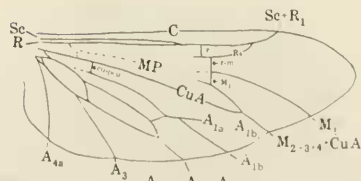
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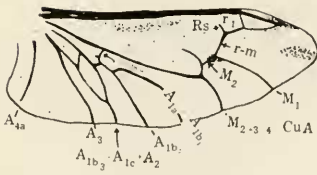
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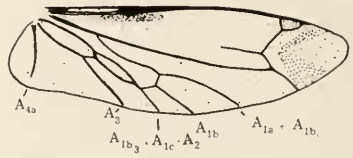
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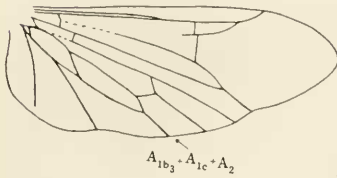
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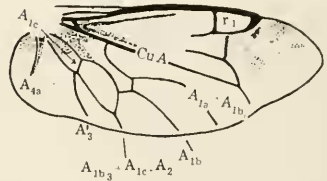
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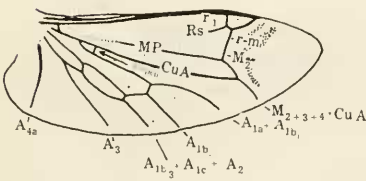
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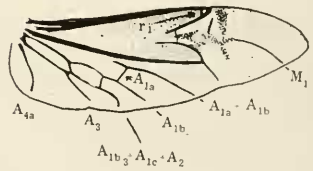
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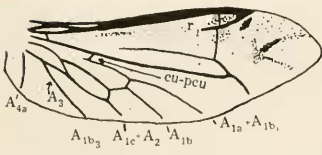
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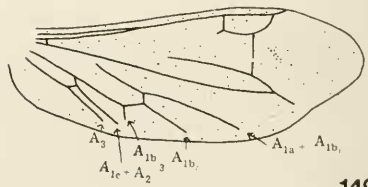
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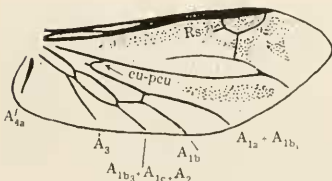
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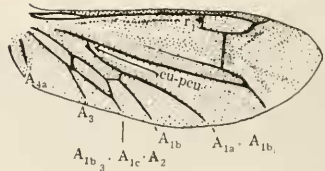
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Both patterns represented by the two genera possess elements representative of a generalized pattern. This involves primarily the occurrence of a number of anal veins none of which are fused apically.

As compared to the Elateroidea, this group is more highly specialized in the reduction of both MP and the 2+3 cell.

Buprestoidea (Figs. 65–72).—The Buprestidae (Fig. 68) represent the generalized pattern for this group. This pattern shares in common with the Dermestoidea the possession of a free A_{1b3} . In addition, there is also a fusion of A_{1a} and A_{1b1} with subsequent fusion proximally of these veins resulting in the loss of the free portion of the proximal segment A_{1a} . In comparison to the Elateroidea (Figs. 75, 87, 95), the buprestid pattern shares with the Dermestoidea the proximal atrophy of MP. In this group, due to the type of specialized anal pattern, there develops a characteristic three forked venational configuration, the composition of which includes the Pcu, the completely fused $A_{1a} + A_{1b1}$ and A_{1b2} . This configuration originates as a result of the loss of any recognizable free portion of A_{1a} and with the incorporation of the free portion of A_{1b1} as a part of this pattern. Following the line of specialization in the Buprestidae, there is a retention of the three forked venational configuration accompanied by a fusion of A_{1b3} with that of $A_{1c} + A_2$. This results in the formation of the characteristic W cell (Fig. 69). Both the Dascillidae (Fig. 71) and the Rhipiceridae (Fig. 72) possess a pattern which closely parallels this line of specialization.

Elateroidea–Cantharoidea (Figs. 73–97).—The Cebriionidae and Elateridae represent a pattern which possesses a generalized 2+3 cell and a well developed MP. In the preanal area, the possession of a generalized 2+3 cell is based upon the interpretation that the r_1 crossvein is considerably proximal to the r -m and M_2 serial appearing crossvein. In comparison, the specialized condition is the loss of r_1 and retention of r_2 thus reducing the size of the 2+3 cell.

Although the anal pattern of any one of the generalized families of the Elateroidea appears to have undergone certain specialization, the study of the pattern of variation in the Lampyridae (Figs. 89–90), indicates that a comparative pattern of the Elateroidea (Fig. 74) is as generalized as any of the Buprestidae or Dermestidae.

Forbes (1922) illustrated an individual variation in a species in Cebrioni-

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Figs. 141–150. 141, *Dinapate wrighti* Horn (Bostrichidae). After Forbes, 1922. 142, Tenebrionoidea comparative pattern. 143, *Tenebrio molitor* L. (Tenebrionidae). 144, *Capnochroa fuliginosa* (Melsheimer) (Alleculidae). 145, *Synchroa punctata* Newman (Melandryidae). 146, *Arthromacra aenea* (Say) (Lagriidae). 147, *Cypherotylus boisduvali* Chevrolat (Erotylidae). 148, *Temnochila virescens* (F.) (Ostomidae). 149, *Languria mozardi* Latreille (Languriidae). 150, *Acropteroxys gracilis* Newman (Languriidae).

dae, in which A_1 consisted of three branches (Fig. 79). He further established this as part of the hypothetical anal pattern of Coleoptera. In addition, based on tracheation, he considered that Coleoptera in general lost the anterior branch designated here as $A_{1a}+A_{1b_1}$ except in the higher Chrysomeloidea. In this case he considered Pcu lost and $A_{1a}+A_{1b_1}$ retained.

A more detailed study of *Scaptolenus lecontei* (Sallé) revealed an additional specialization involving the forking of A_{1b_2} (Fig. 82) as well as the unstable condition consisting of a loss of either the anterior or posterior branches of $A_{1a}+A_{1b_1}$ or A_{1b_2} (Figs. 80–81, 83–84). Such studies indicate the pattern selected by Forbes would not be the generalized venational pattern of this family. The Cebrionidae therefore closely parallel the Lampyridae and Elateridae.

Specialization within the Elateroidea include the following:

1. A fusion of A_{1b_2} with A_{1b_3} as paralleled by the Lampyridae (Figs. 88–90).

2. A loss of any recognizable segment of R_s proximal to the r_1 crossvein as represented by the Phengodidae (Fig. 93).

3. As discussed previously, the possibility of the serial arrangement of a part of Pcu and a $cu-pcu$ crossvein as represented by the Lampyridae (Fig. 87).

4. Both Perothopidae (Fig. 96) and Eucnemidae (Fig. 97) share a common venational pattern distinguished by the fusion $A_{1a} + A_{1b_1}$ with Pcu resulting in a loss of the free distal branch of A_{1a} .

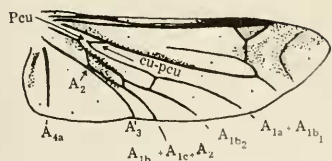
5. The Lycidae–Cantharidae (Figs. 94–95) line of specialization involves the loss of A_{1b_3} as paralleled by the Elateridae (Fig. 92).

6. In the Cantharidae (Fig. 95), there is the loss of the branch A_3 .

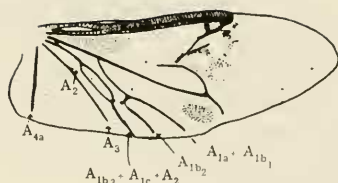
Dryopoidea–Byrrhidae (Figs. 98–105).—In comparing the Elmidae pattern (Fig. 98) to that of Elateridae (Fig. 91), it is noted that the two groups have much in common in relation to the anal venation. The 2+3 cell is more generalized in the Elateridae and approaches more the pattern of the specialized members in the Dryopoidea (i.e. Psephenidae). The families included in this group share the retention of six apparent veins occurring in the anal area (Pcu , $A_{1a}+A_{1b_1}$, A_{1b_2} , $A_{1b_3}+A_{1c}+A_2$, and A_{4a}). Although the Elmidae possess a generalized anal pattern, in the same respect the 2+3 cell is more specialized than that of Ptilodactylidae, Psephenidae and Chelona-

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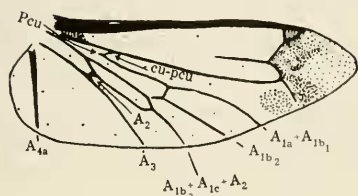
Figs. 151–160. 151, *Melittomma sericeum* Harris (Lymexyidae). 152, *Lecontia discicollis* (LeConte) (Salpingidae). 153, *Cephaloon lepturides* Newman (Cephaloidea). 154, *Cephaloon lepturides* Newman (Cephaloidea). Proximal relationship of Pcu to A_{1a} . 155, *Monomma auberti* Oberthur (Monomatidae). 156, *Mycetophagus californicus* Horn (Mycetophagidae). 157, *Sisenes championi* Horn (Oedemeridae). 158, *Nacerda melanura* (L.) (Oedemeridae). 159, *Pedilus collaris* (Say) (Pedilidae). 160, *Neopyrochroa femoralis* LeConte (Pyrochroidae).



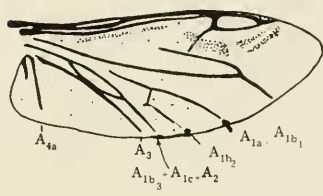
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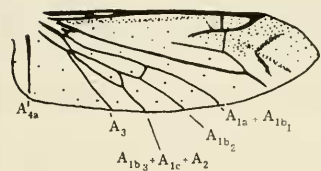
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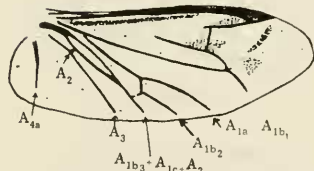
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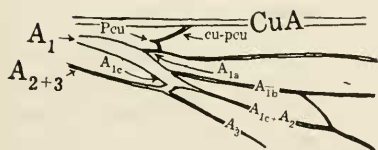
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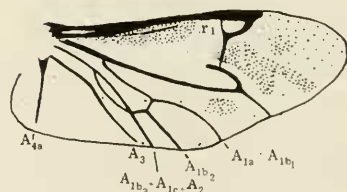
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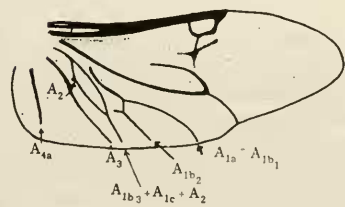
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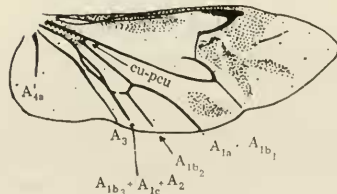
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riidae. From the generalized Dryopoidea pattern the following specializations occur:

1. In the Dryopidae the loss of the r crossvein opens the cell $2+3$ proximally. In the anal venation, there is a loss of the free portion of A_{1a} . In addition there is the loss of the free proximal portion of A_{1b_1} (Fig. 100). This results in the characteristic three pronged configuration paralleled in the Buprestidae (Fig. 69).

2. In the Ptilodactylidae (Fig. 102, specialization has occurred with the loss of the free portion of A_2 resulting in a change in the configuration of the W cell. In addition, there is the loss of a portion of Pcu . It is noted that this family does share with the Elmidae a retention of the free portion of A_{1a} and A_{1b_1} .

3. The remaining families, although possessing a generalized $2+3$ cell, have the most highly specialized anal venation of the group. These include the Chelonariidae (Fig. 103) and the Psephenidae (Fig. 104), both of which share the loss of the W cell. There is the loss of the segment of A_{1c} as paralleled in both the Cerambycidae (Figs. 113–114) and the Cucujidae–Curculionidae (Figs. 120, 122). This consists of a fusion of A_{1b_3} and $A_{1c}+A_2$ resulting in the complete loss of the W cell. Furthermore there is a tendency toward the fusion of A_{1b_2} to $A_{1a}+A_{1b_1}$, accompanied by a loss of the free segment of A_{1b_1} .

4. As in the Ptilodactylidae, the Psephenidae have lost the free portion of A_2 .

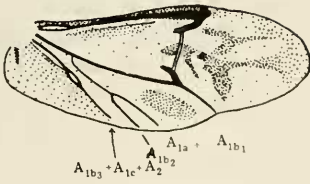
5. The Byrrhidae parallel much of the pattern exhibited by both the Chelonariidae and the Psephenidae.

It is apparent that, even though this group shares a common pattern, the relationship in regard to comparing the generalized and specialized features of each of the families indicates a somewhat heterogeneous group.

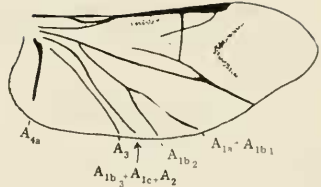
Cerambycidae–Sphindidae (Figs. 106–118).—As a result of the possession of separate A_{1a} and A_{1b_1} distal branches, the Cerambycidae generalized venational pattern consists of seven apparent veins in the anal region. In comparison to the apparent eight-vein generalized pattern of the Dermestidae, which also possess a separate A_{1a} and A_{1b_1} branches, the reduction to seven veins in Cerambycidae is due to the fusion of $A_{1b_3} + A_{1c} + A_2$.

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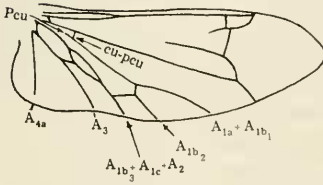
Figs. 161–170. 161, *Anthicus biguttulus* LeConte (Anthicidae). 162, Pyrochroidae, Rhipiphoridae and Meloidae composite pattern. 163, *Geoscopus murinus* Gerstaecker (Rhipiphoridae). After Selander, 1957. 164, *Toposcopus wrighti* LeConte (Rhipiphoridae). After Selander, 1957. 165, *Nephrites* sp. (Rhipiphoridae). After Selander, 1957. 166, *Pelecotoma flavipes* Melsheimer (Rhipiphoridae). After Selander, 1957. 167, *Ptilophorus dufouri* (Latreille) (Rhipiphoridae). 168, *Pediloytta* sp. (Meloidae). After Selander, 1954. 169, *Epicauta marginata* (F.) (Meloidae). 170, *Glipodes sericans* (Melsheimer) (Mordellidae).



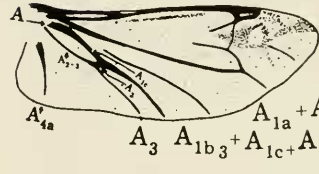
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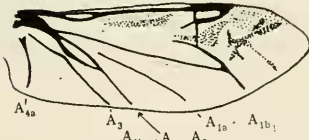
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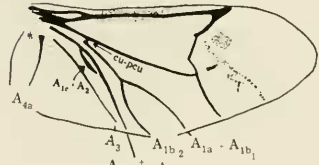
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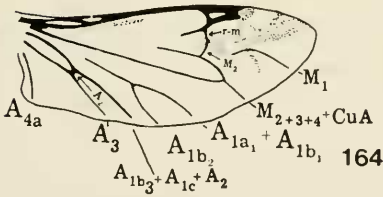
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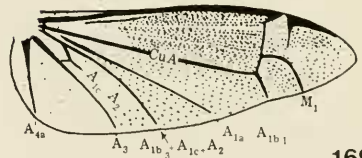
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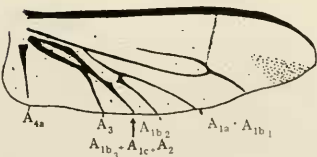
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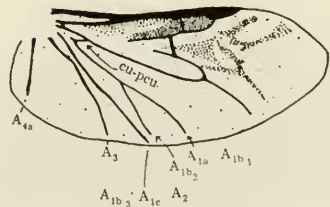
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The Sphindidae (Fig. 118) parallel much of the venational pattern of the specialized members of the Cerambycidae (Figs. 112–113). This includes the following:

1. A sharing of six apparent veins in the anal area due to a complete fusion of A_{1a} to A_{1b_1} .
2. The loss of the free distal segment of A_{1a} resulting in the fusion of $A_{1a} + A_{1b_1}$ to Pcu .
3. The possession of the W cell as a result of the fusion of A_{1b_3} to $A_{1c} + A_2$.
4. The retention of a well developed spurious M_1 vein.

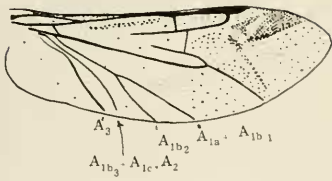
Colydiidae (Fig. 119).—Although there may be only traces of M_1 , this family is included here largely on the basis of sharing a common anal pattern with the Sphindidae. However, even though the Colydiidae possess the six apparent anal patterns as well as the loss of the free portion of A_{1a} due to the fusion of $A_{1a} + A_{1b_1}$ with Pcu , there is in contrast to the Sphindidae line of development, the possession of a more generalized W cell.

Byturidae–Biphyllidae (Figs. 125–130).—Studies conducted by King (1951) involving members of the family Colydiidae, led to a construction of a number of hypothetical wing patterns, indicating relationships shared between the generalized and specialized patterns within this particular family. Using such a parallel study, it became evident that such specialized patterns, as exhibited by the Byturidae, Biphyllidae and possibly even the Coccinellidae and Endomychidae could be traced to sharing in common the pattern associated with the Sphindidae–Colydiidae series.

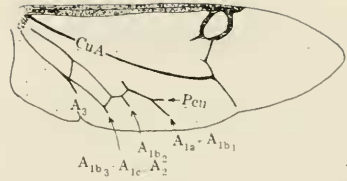
As paralleled by venational patterns of the more specialized members of the family Colydiidae (Figs. 131–132), the Byturidae–Biphyllidae share with the Cerambycidae, Sphindidae, and the generalized venation of the Colydiidae the loss of the free distal portion of A_{1a} (Figs. 126–127). Following the pattern of specialization involving the loss of A_{1b_3} (Fig. 125), a reduction from six apparent veins in the anal region to five is the result of the atrophy of the free apical branch of Pcu distal to where Pcu fuses with $A_{1a} + A_{1b_2}$ (Figs. 126–127). Such a condition can be seen in the Cryptophagidae (Fig. 121) and Curculionidae (Fig. 123).

In addition, there is a fusion of a segment of $A_{1b_{1,2}}$ to $A_{1b_3} + A_{1c} + A_2$ for a short distance proximally. A_{1b_1} and A_{1b_2} anal veins. There is the loss of the distal emerging free segment of A_{1b_1} . Additional specializations which are

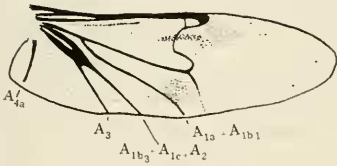
Figs. 171–180. 171, *Glipa hilaris* (Say) (Mordellidae). 172, *Othnius umbrosus* LeConte (Othniidae). 173, *Cymatodera bicolor* Say (Cleridae). 174, *Chariessa pilosa* Forster (Cleridae). 175, *Trichodes nutalli* Kirby (Cleridae). 176, *Necrobinus defunctorum* Walll (Cleridae). After Crowson, 1955. 177, *Melyris abdominalis* F. (Melyridae). After Kempers, 1923. 178, *Collops quadrimaculatus* (F.) (Melyridae). 179, *Spermophagus hoffmanseggii* Gyllenhal (Bruchidae). 180, *Vrilletta decorata* Van Dyke (Anobiidae).



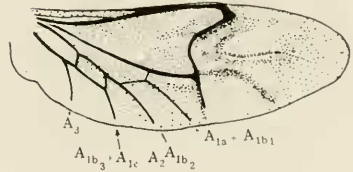
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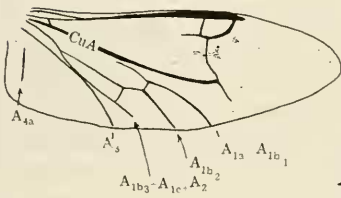
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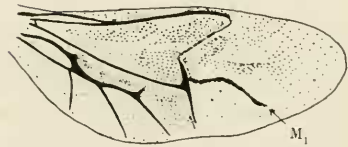
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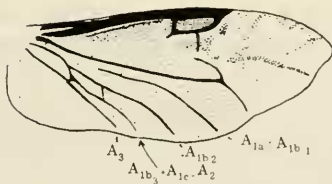
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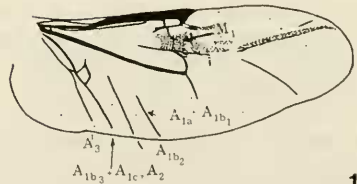
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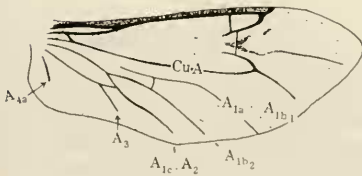
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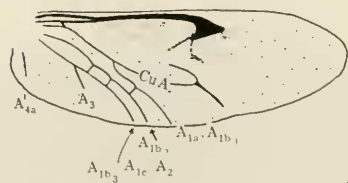
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a part of the Byturidae–Biphylidae pattern are the fusion of A_3 to the degree whereby it becomes a part of the fused $A_{1c}+A_2$ vein and a reduction in A_{4a} (Fig. 131).

The Coccinellidae–Endomychidae line (Figs. 134–136) possesses a highly reduced anal venation which is difficult to trace. The following discussion is included as an example of the possibility of interpreting a highly reduced venational pattern as a result of observing parallel venational trends in available family serial studies (i.e. the Colydiidae–Byturidae–Biphylidae series).

The Coccinellidae retain a well developed M_1 and possible traces of R_2 and R_3 . On this basis alone one would assume that such a pattern is a remnant of a more generalized venation, rather than traceable to any highly specialized present-day form as would be the case in a study of the anal venation. Recognizing this possibility, it is still possible to trace the reduced anal venation by comparison to forms which appear to possess parallel patterns. Therefore, in comparison to the specialized colydiid pattern (Fig. 133), the coccinellid anal pattern (Fig. 135) consists of a proximal segment of the fused veins of Pcu , A_{1a} and A_{1b_1} and a distal apical free portion of $A_{1a}+A_{1b_1}$. There is the loss of the free portion of the vein A_{1b_2} . The remaining distal spur is therefore $A_{1b_3}+A_{1c}+A_2$. Proximally a spur of the secondary branch A_{1b} is retained. In addition, there is the complete loss of A_{4a} .

Chrysomelidae–Bostrichidae (Figs. 137–143).—There is a trend of specialization exhibited by a large share of the families in the remaining discussion in which there is a reduction of six apparent veins in the anal region (Pcu , $A_{1a}+A_{1b_1}$, A_{1b_2} , $A_{1b_3}+A_{1c}+A_2$, A_3 and A_{4a}) to five. This reduction in the number of anal veins is based upon the retention of a free A_{1c} and the loss of Pcu as paralleled for example in such families as the Rhipiceridae (Fig. 72) and Cucujidae (Fig. 120).

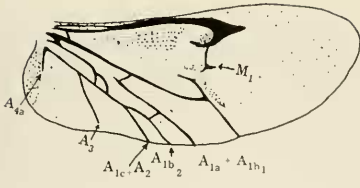
Therefore the selected generalized anal pattern of the Bostrichidae and Chrysomelidae consists of five apparent veins accompanied by the presence of a well defined W cell.

In comparing the two patterns of venation, it is noted that the Bostrichidae have retained a well developed M_1 . In the anal pattern of Bostrichidae (Fig. 141) there is the loss of the free proximal segment of A_{1b_1} .

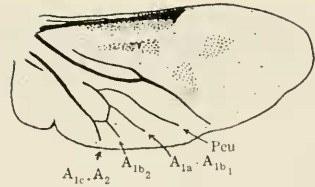
Cucujidae–Curculionidae (Figs. 120–124).—The generalized pattern of these families consists of the retention of six apparent veins in the anal area

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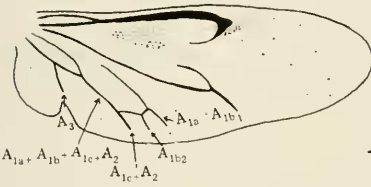
Figs. 181–190. 181, *Trichodesma gibbosa* (Say) (Anobiidae). 182, *Nicobium castaneum* (Olivier) (Anobiidae). 183, *Ptinus brunneus* Duftschmid (Ptinidae). 184, *Bostrichus bicornis* (Weber) (Bostrichidae). 185, *Lyctus planicollis* LeConte (Lyctidae). 186, *Pactopus horni* LeConte (Throscidae). After Forbes, 1922. 187, *Lissomus bicolor* Chevrolat (Throscidae). 188, *Tesserocerus beltii* Sharp (Platypodidae). 189, *Arrhenodes minutes* (Drury) (Brentidae). 190, *Phloeoborus rudis* Erickson (Scolytidae).



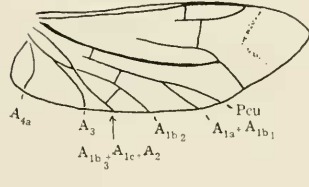
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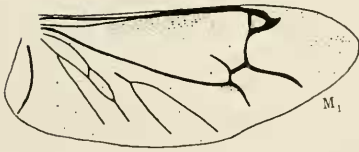
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accompanied by the loss of any trace of the characteristic wedge cell pattern. The developmental stages leading to the disappearance of the wedge cell pattern is closely paralleled by the specialization trends in the Cerambycidae (Figs. 112–114). Such a pattern, leading to the loss of the W cell, is the result of a separate line of specialization involving the fusion rather than the loss of the vein A_{1b_3} to $A_{1c} + A_2$, with the subsequent loss of the free branch designated as A_{1c} .

Tenebrionidae, Meloidea, Lymexyloidea, Erotylidae, Trogositidae, Languriidae, Mycetophagidae (Figs. 143–172).—Aside from the Adepaga, the generalized families of this series represent one of the largest homogeneous groups. In comparison to the Chrysomelidae–Bostrichidae, the veins of the anal region consist of five apparent branches, the free proximal segment of A_{1b_1} , the possession of a well developed W cell and the loss of Pcu. Also a well developed 2+3 cell and MP are retained. Specialization over the Chrysomelidae is primarily in the loss of any recognizable trace of M_1 . The reduction of venation can be traced progressively from family to family within this group and supported with additional evidence of a parallel nature by species selected from certain families. This supportive evidence is used as a parallel comparative guide for interpretation of families which possess highly reduced venation.

Although it is difficult to select any one pattern as basic to the group, the Tenebrionidae (Fig. 143) possess as complete a venational pattern as is represented by any one family. Family specializations are gradual and as a result of the highly specialized venation appear individually to have no connection to any other group.

The trend of specialization is as follows:

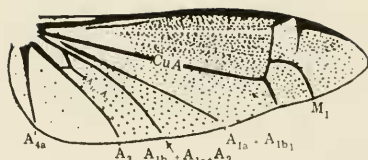
1. Much of the Tenebrionidae pattern is shared by the Alleculidae (Fig. 144), Melandryidae (Fig. 145), Erotylidae (Fig. 147), Trogositidae (Fig. 148), and Languriidae (Fig. 150). The Tenebrionidae and Alleculidae have practically identical patterns except for a slight difference in the configuration of the 2+3 cell and a reduction in the length of MP. In the Erotylidae, Languriidae, and Melandryidae, there is the appearance of a more generalized 2+3 cell. Specialization in the Erotylidae is exhibited in the form of a serial fusion of the cu–pcu crossvein with Pcu. Furthermore, the Erotylidae share a reduction of MP with the Alleculidae and Trogositidae. The

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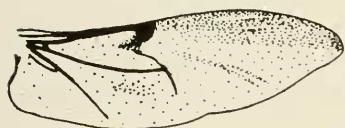
Figs. 191–200. 191, *Eurymycter fasciatus* (Olivier) (Anthribidae). 192, *Anthonomus grandis* Boheman (Curculionidae). 193, *Nosodendron unicolor* Say (Nosodendridae). 194, *Nosodendron unicolor* Say (Nosodendridae). 195, *Peltastica tuberculata* Mannerheim (Derodontidae). 196, *Epicauta marginata* (F.) (Meloidea). 197, *Cephaloon lepturides* Newman (Cephaloidea). 198, *Atractocerus* sp. (Telegeusidae). 199, *Telegeus debilis* Horn (Telegeusidae). 200, *Eoxenos laboulbenei* Peyerimhoff (Stylopidae). After Bohart, 1941.



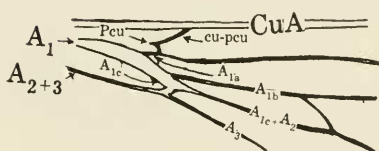
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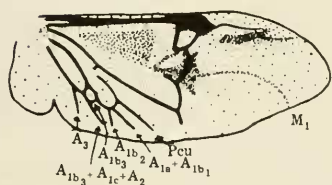
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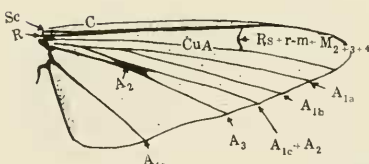
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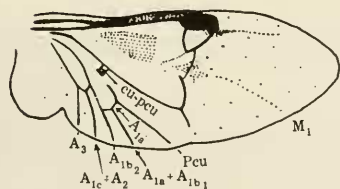
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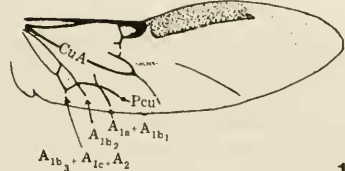
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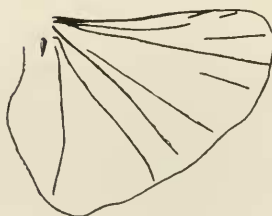
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Trogositidae have lost any connection of Pcu with CuA and possess a highly reduced 2+3 cell. In the same respect, the generalized condition, involving the retention of traces of apical venation, appears in the Trogositidae.

2. The Lymexylidae (Fig. 151) and Salpingidae (Fig. 152) share both a reduction of the 2+3 cell and a tendency toward the atrophy of the free branch of A_2 .

3. The Cephaloidea (Fig. 153) possess a venation which in respect to the retention of the proximal portion of A_{1a} , is more generalized than any member of this group. A significant configuration of this pattern (Fig. 154) is the retention of a proximal postcubital spur accompanied by the attachment of Pcu to CuA via a cu-pcu crossvein. Such a condition is evidence that in Coleoptera Pcu has as its attachment to CuA the alignment of a cu-pcu crossvein to that of the proximal portion of Pcu. Specializations involve the loss of any proximal connection of Pcu and a reduction in both MP and the free segment of the branch A_2 .

4. From the Lagriidae (Fig. 146) to the more specialized families, there is a distal narrowing of the W cell. This is due to the further fusion of A_{1b_3} with $A_{1c} + A_2$.

5. In addition to the W cell becoming narrow distally, the Monommatidae (Fig. 155), Mycetophagidae (Fig. 156), Oedemeridae (Figs. 157-158), Pedilidae (Fig. 159) and Pyrochroidae (Fig. 160) also share a proximal narrowing of the W cell. This is due primarily to a retention of the branch A_{1c} accompanied by the gradual atrophy of the free branch of A_2 .

6. There is in the Pyrochroidae (Fig. 160) the loss of the r crossvein as paralleled in certain members of the Oedemeridae (Fig. 158).

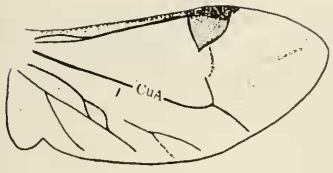
7. There appears in the Oedemeridae, Pyrochroidae, Mycetophagidae and Monommatidae an interruption in the free branch of $A_{1b_1} + A_{1b_2}$.

8. The Anthicidae (Fig. 161) closely parallels the pattern of the Pyrochroidae. Specialization involves the loss of a free portion of $A_{1b_1} + A_{1b_2}$, the loss of the Pcu spur and the atrophy of A_3 .

9. A composite pattern (Fig. 162) including components from the Pyrochroidae (Fig. 160), Rhipiphoridae (Fig. 163) and Meloidae (Figs. 168-169) serve as a basis for the discussion of the remaining highly specialized members. These are as follows:

a. In the Rhipiphoridae the specialized members of this family indicate

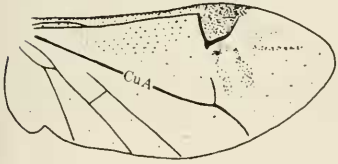
Figs. 201-210. 201, *Eucinetus terminalis* LeConte (Eucinetidae). 202, *Scirtes tibialis* Guerin (Helodidae). 203, *Elonus nebulosus* (LeConte) (Euglenidae). 204, *Rhizophagus cylindricus* LeConte (Rhizophagidae). 205, *Pityophagus rufipennis* Horn (Nitidulidae). 206, *Sphaerites glabratus* (F.) (Sphaeritidae). 207, *Lepicerus horni* Sharp (Lepiceridae). 208, *Syntelia histeroides* Lewis (Synteliidae). 209, *Scaphidium quadriguttatum* Say (Scaphidiidae). 210, *Agathidium oniscoides* Beauvois (Leiodidae).



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- there is a loss of the free portion of $A_{1b_1} + A_{1b_2}$ accompanied by a loss of A_{1b_2} and the free portion of A_{1b_1} .
- b. Although the Meloidae share much in common with the Pyrochroidae, certain members of this family retain a free segment of A_2 . Specialization has resulted in the loss of the free portion $A_{1b_1} + A_{1b_2}$, the loss of the r crossvein and the loss of a segment of $A_{1c} + A_2$. The latter results in the appearance of the W cell being open distally.
 - c. The Mordellidae (Figs. 170–171) possess a highly specialized anal pattern, paralleling much of the venation noted in the more specialized members of the Rhipiphoridae (Fig. 166). It is noted, however, that even though the anal pattern is highly reduced, the preanal 2+3 cell is as generalized as any of the Tenebrionidae.
 - d. The highly reduced venation of the Othniidae (Fig. 172) is traceable only as a result of a study of the parallel line of development in the Rhipiphoridae (Fig. 167).

SUPPLEMENTARY FAMILIES

The remaining families under consideration are included here because it is believed that either further detailed investigation is necessary to resolve the nature of the generalized pattern or a more detailed serial study may reveal a parallel path of specialization leading to families which possess comparably reduced venational patterns.

Cleridae (Figs. 173–176).—As a result of an investigation conducted within this family, as well as the evidence presented by Forbes (1922), the generalized pattern selected for the family Cleridae consists of an apparent five-branched pattern in the anal area as well as the characteristic W cell. Such a pattern would suggest that the Cleridae be included in the Tenebrionoidea group (i.e. Trogoxetidae, Erotylidae, etc.).

Crowson (1955) states that the basic type of wing venation does not seem to differ greatly from Dermestoidea or Cucujoidea. He illustrates as representative of this pattern *Necrobilus defunctorum* Waltl (Fig. 176). This pattern possesses an apparent six branches in the anal region in addition to the W cell. Such a pattern would suggest a close affinity to Colydiidae.

Melyridae (Figs. 177–178).—The Melyridae appear to possess a venation which is difficult to compare to any other group but as suggested by Forbes

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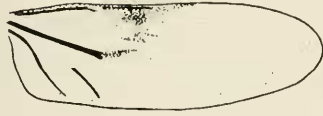
Figs. 211–220. 211, *Nemadus parasitus* LeConte (Leptodiridae). 212, *Brathinus nitidus* LeConte (Brathinidae). 213, *Faronus* sp. (Pselaphidae). 214, *Phalacrus penicillatus* Say (Phalacridae). 215, *Georyssus californicus* LeConte (Georyssidae). After Forbes, 1926. 216, *Clambus minutus* Sturm (Clambidae). After Crowson, 1955. 217, *Heteroceris ventralis* Melsheimer (Heteroceridae). 218, *Aeratrachis* sp. (Ptilidae). 219, *Melanophthalma distinguenda* Comolli (Lathridiidae). 220, *Cis fuscipes* Mellié (Cisidae).



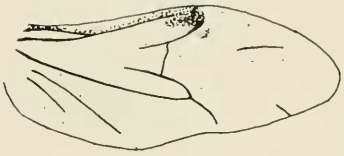
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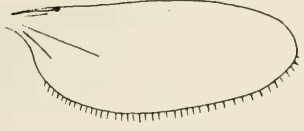
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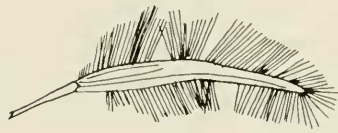
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(1922) may share a pattern common to the Coccinellidae. Kempers (1923) illustrated a melyrid pattern (Fig. 177), which would suggest that such a venation closely parallels the pattern established for the Tenebrionoidea.

Bruchidae—Anobiidae (Figs. 179–182).—Both retain the M_1 spurious vein and share in common a pattern similar to that of the Sphindidae as well as the Chrysomelidae and Bostrichidae.

Ptinidae (Fig. 183).—Forbes (1922) discusses this family as closely resembling the Bostrichidae (Fig. 184). A study of the Anobiidae (Figs. 180–182) reveals a possible line of specialization (i.e. loss of A_{1b_2}) along which the present-day Ptinidae pattern may have developed.

Lyctidae (Fig. 185).—The venational pattern for this family possesses a highly reduced anal pattern but a well developed M_1 . Both the well developed M_1 as well as the configuration of the radial cell suggests a close affinity to the Bostrichidae (Fig. 184).

Throscidae (Figs. 186–187).—A study of this group led to a venational pattern similar to that proposed by Forbes (1922). However, such a reduced pattern did not suggest any close relationship to any other group. Kempers (1923) has illustrated a wing (Fig. 187) as a member of the family Throscidae. This would suggest a pattern closely paralleling the Elateroidea.

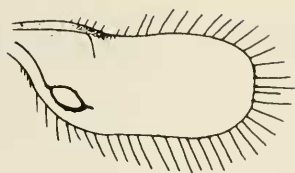
Helotidae (Fig. 124).—The configuration of the radial cell, specialization involving the loss of the distal branch of Pcu , and the absence of both the free segment of A_{1c} and the wedge cell all indicate a specialized pattern closely allied to the Cucujidae—Curculionidae venation.

Platypodidae—Brentidae—Scolytidae—Anthribidae (Figs. 188–192).—The configuration of the radial cell, M_1 and $M_{3+4} + CuA$ indicate the close relationship of these families to that of the Cucujidae—Curculionidae.

Nosodendridae—Derodontidae (Figs. 193–195).—The retention of Pcu , M_1 , as well as the configuration of the radial cell and anal veins, all suggest a relationship to the Dermestidae. At present, research is being carried out to further clarify the relationship of these and other families to that of the Dermestidae.

Telegeusidae (Fig. 199).—Although *Telegeus debilis* Horn is highly reduced, it is the genus *Atractocerus* which possesses a venation that is distinctive as well as problematic in determining the exact relationship of this family to any other family in Coleoptera. King (1955) on the basis of multiple characteristics, including wing venation, erected a separate suborder, the Apicalae, for the inclusion of this genus. On the basis of a series of hypothetical stages proposed by Selander (1959), Arnett (1968) accepts *Atractocerus* as a part of Telegeusidae, stating that such a proposal disproves the concepts presented by King.

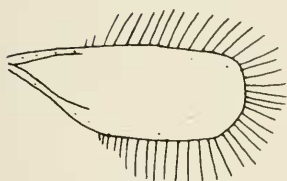
Based upon the relationship of Coleoptera to Megaloptera, the use of the fossil protoperlarian comparative pattern and the proposed trends of spe-



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Figs. 221–225. 221, *Sphaerius politus* Matthews (Sphaeriidae). 22, *Hydroscapha* sp. (Hydroscaphidae). 223, *Micromalthus debilis* LeConte (Micromalthidae). After Forbes, 1926. 224, *Limnebius piceus* Horn (Limnebiidae). 225, *Sericoderus lateralis* (Gyllenhal) (Orthoperidae).

cialization, the following is a discussion on the venational pattern of *Atractocerus* (Fig. 198):

1. C, Sc, and R are present.
2. Due to the consistent venational feature present in even the highly specialized patterns of Coleoptera, the prominent longitudinal vein posterior to the radius is designated CuA.
3. The transverse appearing vein connecting radius to CuA consists of a serial connection of Rs, r-m crossvein, M₂ and M₃₊₄. This is, as recognized by Selander, a specialization common to such families as the Meloidae (Fig. 196).
4. The anal venation possesses a more generalized pattern in contrast to the preanal area. The anal pattern proposed is as follows:
 - a. A_{1a} fuses proximally with Pcu. In comparison to the parallel proximal

pattern illustrated by the Cephaloidae (Fig. 197), there is an atrophy of cu-pcu crossvein accompanied by a further atrophy of the remaining free proximal segment of Pcu.

- b. A_{1a} emerges distally as a free branch.
- c. The secondary branch A_{1b} fuses a short distance with A_{1a} , after which it emerges distally as a free branch.
- d. A_{1c} branch coalesces with A_2 which emerges as the fused vein $A_{1c}+A_2$ running to the margin of the wing. With the fusion of A_{1c} to A_2 there is the loss of the free segment of A_2 as paralleled in such families as the Lymexylidae (Fig. 151) and Salpingidae (Fig. 152). A remnant of this fusion is seen as a thickening between $A_{1c}+A_2$ and A_3 . Following this fusion, A_3 emerges as a free vein running to the margin of the wing. The remaining branch is that of A_{4a} .
- e. The proximal relationship involved A_{1a} , A_{1b} and A_{1c} is as generalized as any of the coleopterous patterns studied to date. Such an arrangement parallels in many features the anal pattern occurring in the Megaloptera.

In summary, *Atractocerus* has retained a remnant of what was once a generalized venational pattern. This is seen primarily in the proximal relationship of A_{1a} , A_{1b} and A_{1c} .

CONCLUSION

Specializations within the Coleoptera involve an overall trend toward a reduction in venation. In addition there is a reduction in the crossvein pattern replaced in many situations by a fusion of the longitudinal veins. Additional studies will probably reveal the latter to be more pronounced than indicated in this investigation.

The Cupedidae-Adephaga preserve a generalized preanal pattern comparable to the parallel cellular pattern of the Sialidae. Although introduced for discussion purposes, the preanal cellular pattern is an established part of the generalized coleopterous venation. In turn, this pattern is additional evidence of the affinity Coleoptera has for a neuropteroid type of venation (i.e. a pattern paralleled in such families as the Sialidae as well as the suborder Raphidioidea).

The Scarabaeidae and Hydrophilidae serve as guides to the configuration of the apical venation.

In general many of the family relationships involve a comparison of the anal pattern. Family relationships are in accordance with how they are presented in the discussion. Furthermore, it is emphasized that although the trends of specialization are indicative of the order as a whole, many are the result of the development of parallel patterns (i.e. anal venation of Adephaga and Tenebrionidae).

From a composite study of both the Adephaga and Polyphaga, the anal

venation consists of what is regarded for purposes of discussion as nine apparent anal branches. These are respectively: P_{cu} , A_{1a} , A_{1b_1} , A_{1b_2} , A_{1b_3} , $A_{1c}+A_2$, A_3 , A_{4a} and A_{4b} . Using the nine apparent anal branches as a basis, the following is a summary of the trends of specialization as represented by selected family patterns:

1. In the Cupedidae–Adephaga, there is a reduction from nine apparent to seven apparent veins in the anal area. This is due to a fusion of $A_{1a}+A_{1b_1}$ and A_{1b_3} to $A_{1c}+A_2$. The latter fusion resulting in the formation of a wedge cell (W).

2. In the Scarabaeidae and Hydrophilidae, there is a retention of A_{4b} , while in the remaining Polyphaga, there appears to be an atrophy of this vein. This reduces the number in the generalized polyphagan pattern to an apparent eight veins.

3. The Staphyloidea line of development, in comparison to the specialized members of the Scarabaeidae, possesses a highly reduced venation, making it difficult to determine the affinities of this group to any of the other present-day coleopterous series.

4. The Dermestidae–Buprestidae retain a free A_{1b_3} secondary branch. The Dermestidae retain the generalized polyphagan pattern of eight apparent veins in the anal region, while due to a fusion of A_{1a} to A_{1b_1} , the Buprestidae have undergone a reduction to an apparent seven veins in the anal area.

5. In the Cerambycidae generalized pattern there is a retention distally of an independent A_{1a} and A_{1b_1} . A reduction to seven veins in contrast to the generalized Buprestidae is due to a fusion of A_{1b_3} to $A_{1c}+A_2$ resulting in the characteristic W cell as paralleled in the Cupedidae–Adephaga.

6. The Elateroidea–Cantharoidea–Dryopoidea exhibit a reduction from eight to six apparent veins in the anal area. This is due to a fusion of $A_{1a}+A_{1b_1}$, as paralleled in the Buprestidae and a fusion of A_{1b_3} to $A_{1c}+A_2$ forming the W cell, as paralleled in the Cerambycidae.

7. The Chrysomelidae–Bostrichidae, Tenebrionoidea, as well as the families included in the Adephaga have reduced the number of apparent veins in the anal area to five. This reduction incorporates the fusion of A_{1a} to A_{1b_1} , and the loss of P_{cu} .

8. The Cucujidae–Curculionidae series consists of six apparent veins in the anal area. As paralleled in the Elateroidea–Cantharoidea–Dryopoidea line of development, there is a fusion of A_{1a} to A_{1b_1} , as well as a fusion of A_{1b_3} to $A_{1c}+A_2$. Although the Cucujidae–Curculionidae possess six apparent veins in the anal area, there is the complete absence of any wedge cell. Thus the series consists of a separate line of specialization closely paralleling the Cerambycidae. The loss of the wedge cell does not involve an atrophy of A_{1b_3} as traced in the Elateroidea–Cantharoidea–Dryopoidea but consists of a complete fusion of A_{1b_3} to $A_{1c}+A_2$ resulting in the loss of the free proximal segment of A_{1c} .

The approach used in the study was based upon evidence gathered from the following sources: 1) Comparative studies conducted within the orders Coleoptera and Neuroptera; 2) Studies of individual variation in species of both the Coleoptera and the suborder Megaloptera; 3) Serial studies of families available in the literature as well as those available in the E. W. King collection; and 4) A review of selected sources of paleoentomological literature.

Certain families having highly reduced venation were included (i.e. Coccinellidae) to emphasize the possibilities involving the use of serial studies as parallel guides in determining the line of specialization along which such highly reduced venational patterns developed.

Due to the fact that some families are represented by only a single species, the venation illustrated is not necessarily representative of a generalized venation.

It is concluded, however, that the approach followed and the conclusions reached in this study will eventually lead to a better understanding of the venational affinities which exist among the alate insect orders.

LIST OF FAMILIES

The following list of families of Coleoptera is arranged as they occur in the discussion. Included is a list of families not discussed due to insufficient number of specimens for the determination of the type of comparative pattern (Figs. 201-208), highly reduced venation (Figs. 200, 209-225), or unavailability of a specimen.

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|-------------------|---------------------|--------------------|
| 1. Cupedidae | 25. Phengodidae | 49. Alleculidae |
| 2. Gyrinidae | 26. Perothopidae | 50. Melandryidae |
| 3. Dytiscidae | 27. Eucnemidae | 51. Erotylidae |
| 4. Amphizoidae | 28. Lycidae | 52. Trogoxetidae |
| 5. Hygrobiidae | 29. Cantharidae | 53. Languriidae |
| 6. Noteridae | 30. Elmidae | 54. Lymexylidae |
| 7. Rhyssodidae | 31. Dryopidae | 55. Salpingidae |
| 8. Haliplidae | 32. Ptilodactylidae | 56. Cephaloidea |
| 9. Carabidae | 33. Chelonariidae | 57. Lagriidae |
| 10. Cicindelidae | 34. Psephenidae | 58. Monommatidae |
| 11. Hydrophilidae | 35. Byrrhidae | 59. Mycetophagidae |
| 12. Lucanidae | 36. Cerambycidae | 60. Oedemeridae |
| 13. Scarabaeidae | 37. Sphindidae | 61. Pedilidae |
| 14. Passalidae | 38. Colydiidae | 62. Pyrochroidae |
| 15. Histeridae | 39. Byturidae | 63. Anthicidae |
| 16. Silphidae | 40. Biphyllidae | 64. Rhipiphoridae |
| 17. Staphylinidae | 41. Coccinellidae | 65. Meloidea |
| 18. Dermestidae | 42. Endomychidae | 66. Mordellidae |
| 19. Buprestidae | 43. Chrysomelidae | 67. Othniidae |
| 20. Rhipiceridae | 44. Bostrichidae | 68. Cleridae |
| 21. Dascillidae | 45. Cucujidae | 69. Melyridae |
| 22. Cebrionidae | 46. Cryptophagidae | 70. Anobiidae |
| 23. Elateridae | 47. Curculionidae | 71. Bruchidae |
| 24. Lampyridae | 48. Tenebrionidae | 72. Ptinidae |

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| 73. Lyctidae | 77. Brentidae | 80. Nosodendridae |
| 74. Throscidae | 78. Scolytidae | 81. Derodontidae |
| 75. Helotidae | 79. Anthribidae | 82. Telegeusidae |
| 76. Platypodidae | | |

Families with insufficient number of specimens.

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|-----------------|----------------|-------------------|
| 83. Stylopidae | 85. Helodidae | 87. Rhizophagidae |
| 84. Eucinetidae | 86. Euglenidae | 88. Nitidulidae |

Families with highly reduced venation.

- | | | |
|------------------|--------------------|---------------------|
| 89. Sphaeritidae | 96. Pselaphidae | 103. Cisidae |
| 90. Lepiceridae | 97. Phalacridae | 104. Sphaeriidae |
| 91. Synteliidae | 98. Georyssidae | 105. Hydroscaphidae |
| 92. Leiodidae | 99. Clambidae | 106. Micromalthidae |
| 93. Leptodiridae | 100. Heteroceridae | 107. Limnebiidae |
| 94. Scaphidiidae | 101. Ptiliidae | 108. Orthoperidae |
| 95. Brathinidae | 102. Lathridiidae | |

Families unavailable for study.

- | | | |
|-----------------------|----------------------|-----------------------|
| 109. Scydmaenidae | 114. Drilidae | 119. Catapochrotidae |
| 110. Limnichidae | 115. Jacobsoniidae | 120. Discolomidae |
| 111. Cerophytidae | 116. Tretothoracidae | 121. Phaenocephalidae |
| 112. Karumiidae | 117. Trictenotomidae | 122. Nilionidae |
| 113. Brachypsectridae | 118. Petriidae | |

LITERATURE CITED

- Arnett, R. H., Jr. 1968. The beetles of the United States. Am. Entomol. Inst. (Ann Arbor), 1112 pp.
- Beal, R. S., Jr. 1967. A revisionary study of the North America dermestid beetles formerly included in the genus *Perimegatoma* (Coleoptera). Misc. Publ. Entomol. Soc. Am. 5(6): 281-312.
- Bohart, R. M. 1941. A revision of the Strepsiptera with special reference to the species of North America. Univ. Calif. Publ. Entomol. 7: 91-159.
- Crowson, R. A. 1964. A revision of the genera of the Chrysomelid group Sagrinae (Coleoptera). Trans. R. Entomol. Soc. Lond. 97(4): 75-115.
- Forbes, W. T. M. 1922. The wing-venation of Coleoptera. Ann. Entomol. Soc. Am. 15(4): 328-352.
- . 1926. The wing folding patterns of the Coleoptera. J. N.Y. Entomol. Soc. 34(1): 42-68; 34(2): 91-139.
- Good, H. G. 1925. Wing venation of the Buprestidae. Ann. Entomol. Soc. Am. 18(2): 251-276.
- . 1929. Wing venation of the Cerambycidae. Unpublished Ph.D. thesis, Univ. of Illinois, 228 pp.
- Graham, S. A. 1922. A study of the wing venation of the Coleoptera. Ann. Entomol. Soc. Am. 15(2): 191-200.
- Hamilton, K. G. A. 1971. The insect wing, part I. Origin and development of wings from pronotal lobes. J. Kans. Entomol. Soc. 44: 421-433.
- . 1972a. The insect wing, part II. Vein homology and the archetypal insect wing. J. Kans. Entomol. Soc. 45: 54-58.

- . 1972b. The insect wing, part III. Venation of the orders. *J. Kans. Entomol. Soc.* 45: 145–162.
- . 1972c. The insect wing, part IV. Venational trends and the phylogeny of the winged orders. *J. Kans. Entomol. Soc.* 45: 295–308.
- Hinton, H. E. 1940. A monographic revision of the Mexican water beetles of the family Elmidae. *Novit. Zool.* 42(2): 217–396.
- Holloway, B. A. 1963. Wing development and evolution of New Zealand Lucanidae (Insecta: Coleoptera). *Trans. R. Soc. N.Z.* 3(11): 99–116.
- Kempers, B. 1923. Das Flügelgeader der Käfer. *Entomol. Mitt.* 12(2): 1–115.
- King, E. W. 1951. Evolution and phylogeny in the Cucujoid Coleoptera. Unpublished Ph.D. thesis, Univ. of Illinois, 95 pp.
- . 1955. The phylogenetic position of *Atractocerus* Palis. *Coleopt. Bull.* 9(5): 65–74.
- . 1956. Wing venation in the Adephaga and its contribution to phylogeny. *Proc. Iowa Acad. Sci.* 63: 697–699.
- Selander, R. B. 1954. Evolution of the Meloidae. Unpublished M.S. thesis, Univ. of Illinois, 86 pp.
- . 1957. The systematic position of the genus *Nephrites* and the phylogenetic relationships of the higher groups. *Ann. Entomol. Soc. Am.* 50(1): 88–103.
- . 1959. Additional remarks on wing structure in *Atractocerus* Palis. *Coleopt. Bull.* 13(1): 1–5.
- Wallace, F. L. and R. C. Fox. 1975. A comparative morphological study of the hind wing venation of the order Coleoptera, Part I. *Proc. Entomol. Soc. Wash.* 77(3): 329–354.
- Ward, R. D. 1979. Chapter 2.23. Pp. 181–191. *In* Erwin, T. L., et al., eds., *Carabid beetles: Their evolution, natural history, and classification*. W. Junk B. V., The Hague, The Netherlands. 635 pp.